Published in the United States of America

2022 • VOLUME 16 • NUMBER 2

AMPHIBIAN & REPTILE CONSERVATION

amphibian-reptile-conservation.org

ISSN: 1083-446X

eISSN: 1525-9153

Front cover: Black-webbed Treefrog (*Rhacophorus kio* Ohler & Delorme 2006), male, Xuan Nha Nature Reserve, Son La Province, Vietnam. This frog is known to occur in China, Myanmar, Thailand, and Vietnam (Frost 2022). It is categorized as Endangered (EN) by the Vietnam Red Data Book (2007). The Black-webbed Treefrog is a threatened species in Vietnam due to habitat degradation and severe habitat fragmentation. This species was found at night, on trees, and near puddles in the evergreen forests. *Photo by Anh Van Pha.*

Introductory page. *Smilisca cyanosticta* (Smith, 1953). The Blue-spotted Treefrog occurs on the Atlantic slopes of southern Mexico and northern Central America from Oaxaca and southern Veracruz through northern Chiapas, Mexico, into Guatemala (https://amphibiansoftheworld.amnh.org). These individuals were located at Ejido Villa Guadalupe, in the municipality of Huimanguillo, Tabasco. Wilson et al. (2013b) determined its EVS as 12, placing it in the upper portion of the medium vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN, but this species is not listed by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

Official journal website:
amphibian-reptile-conservation.org

Amphibian & Reptile Conservation
16(2) [General Section]: 1–61 (e315).

The herpetofauna of Tabasco, Mexico: composition, distribution, and conservation status

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***Abstract.*—The herpetofauna of Tabasco, Mexico, consists of 170 species, including 39 anurans, five caudates, one caecilian, two crocodylians, 111 squamates, and 12 turtles. We catalogued the distribution of these species among the three physiographic regions we recognize in the state: the Gulf Coastal Plain (88 species), the Sierras Bajas de Petén (93 species), and the Sierra Norte de Chiapas (145 species). The individual species are found in either one, two, or all three regions (mean = 1.9). Approximately 68% of the herpetofauna in Tabasco occupies only one or two of the three regions, which is of important conservation significance. The largest number of single-region species is found in the Sierra Norte de Chiapas (50), followed by the Gulf Coastal Plain (12) and the Sierras Bajas de Petén (nine). Coefficient of Biogeographic Resemblance (CBR) calculations indicate that the Sierra Norte de Chiapas and the Sierras Bajas de Petén share the greatest number of species (79), followed by 71 species between the Sierra Norte de Chiapas and the Gulf Coastal Plain, and 61 between the Gulf Coastal Plain and the Sierras Bajas de Petén. Fifty-five species occupy all three regions. A similarity dendrogram based on the Unweighted Pair Group Method with Arithmetic Averages (UPGMA) illustrates that the Sierras Bajas de Petén clusters with the Gulf Coastal Plain at the 0.67 level and the Sierra Norte de Chiapas clusters with the previous pair at the 0.64 level, and overall indicates an intermediate level of similarly. With reference to distributional categories, the greatest number of species is represented by the non-endemic species (146 of 170), followed by the country endemics (20), and the non-natives (five). Of the 146 non-endemic species, the majority (95) are MXCA species (i.e., those found only in Mexico and Central America). The principal environmental threats to the Tabasco herpetofauna are deforestation, agricultural activities, roads, soil contamination and oil extraction, myths and cultural factors (gastronomy), illegal commerce, and forest fires. We evaluated the conservation status of each of the native species by using the SEMARNAT, IUCN, and EVS systems, of which the EVS system provided the most inclusive assessment of the state's herpetofauna. We also employed the Relative Herpetofaunal Priority (RHP) method to determine the rank order of the three physiographic regions and found the highest values in the Sierra Norte de Chiapas. Most of the protected areas in the state are located in the Gulf Coastal Plain, which is only the second or third most important region from a conservation perspective. Nonetheless, about 95% of the native herpetofauna has been documented within the system of protected areas. Finally, we provide a set of conclusions and recommendations for the future protection of the Tabasco herpetofauna.**

Keywords. Anurans, caecilians, caudates, conservation status, crocodylians, physiographic regions, protected areas, protection recommendations, squamates, turtles

***Resumen.*—La herpetofauna de Tabasco, México, consta de 170 especies, incluidos 39 anuros, cinco caudados, un cecílido, dos crocodilianos, 111 escamosos y 12 tortugas. Catalogamos la distribución de estas especies entre las tres regiones fisiográficas que reconocemos, incluyendo la Llanura Costera del Golfo (88 especies), las Sierras Bajas del Petén (93 especies) y la Sierra Norte de Chiapas (145 especies). Las especies individuales se**

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encuentran de una a tres regiones (media = 1,9). Aproximadamente el 68% de la herpetofauna de Tabasco ocupa solo una o dos de las tres regiones, lo que es de gran importancia para la conservación. El mayor número de especies de una sola región se encuentra en la Sierra Norte de Chiapas (49) seguida por la Llanura Costera del Golfo (12) y las Sierras Bajas del Petén (nueve). Los cálculos del Coeficiente de semejanza biogeográfica (CBR) demuestran que la Sierra Norte de Chiapas y las Sierras Bajas de Petén comparten el mayor número de especies (79), seguidas de 71 entre la Sierra Norte de Chiapas y la Llanura Costera del Golfo y 61 entre la Llanura Costera del Golfo y Sierras Bajas del Petén. Cincuenta y cinco especies ocupan las tres regiones. Un dendrograma de similitud basado en el método de grupos de pares no ponderados con promedios aritméticos (UPGMA) ilustra que las Sierras Bajas del Petén se agrupan junto con Llanura Costera del Golfo en el nivel .67 y la Sierra Norte de Chiapas se agrupa con el par anterior en el nivel .64, lo que indica un nivel generalmente intermedio de similitud en general. Con referencia a las categorías de distribución, el mayor número de especies es el de las especies no endémicas (146 de 170), seguido de las endémicas del país (20) y no nativos (cinco). De las 146 especies no endémicas, la mayor parte (95) son especies MXCA. Las principales amenazas ambientales para la herpetofauna de Tabasco son deforestación, actividades agropecuarias, carreteras, contaminación del suelo y actividades petroleras, mitos y factores culturales (gastronomía), comercio ilegal, e incendios forestales. El estado de conservación de cada especie nativa se evaluó mediante el uso de los sistemas SEMARNAT, UICN y EVS, de los cuales el sistema EVS fue de mayor utilidad. También se utilizó el método de Prioridad Relativa de la Herpetofauna (RHP) para determinar el orden de importancia de las tres regiones fisiográficas y los valores más altos se encontraron en la Sierra Norte de Chiapas. La mayoría de las áreas protegidas en el estado están ubicadas en la Llanura Costera del Golfo, que es solo la segunda o tercera región más importante desde una perspectiva de conservación. No obstante, alrededor del 95% de la herpetofauna nativa se ha documentado en el sistema de áreas protegidas. Finalmente, se entregan un conjunto de conclusiones y recomendaciones para la futura protección de la herpetofauna de Tabasco.

Palabras Claves. Anuros, áreas protegidas, caudados, cecílidos, crocodilidos, escamosos, estatus de conservación, recomendaciones de protección, regiones fisiográficas, tortugas

Citation: Barragán-Vázquez MR, Ríos-Rodas L, Fucsko LA, Porras LW, Mata-Silva V, Rocha A, DeSantis DL, García-Padilla E, Johnson JD, Wilson LD. 2022. The herpetofauna of Tabasco, Mexico: composition, distribution, and conservation status. *Amphibian & Reptile Conservation* 16(2): 1–61 (e315).

Received: 9 May 2022; **Accepted:** 21 June 2022; **Published:** 8 August 2022

"The more we get done ourselves, the easier it will be for our children and their children to move the world back to sustainability."

Peter H. Raven (2021)

Introduction

Tabasco is an oddly shaped state in Mexico, in which a western segment and an eastern segment are connected to each other by a slender isthmus. With a total area of 24,731 km^2, this state is relatively small (the 24th smallest of the 32 federal entities in Mexico, http://inegi.org; accessed 5 May 2022). The state's area constitutes only about 1.3% of the country's area. The coastal region of Tabasco lies adjacent to the southwesternmost corner of the Gulf of Mexico. To the southwest, Tabasco is bordered by the state of Veracruz, to the northeast by the state of Campeche, to the south by the state of Chiapas, and to the southeast by a small portion of the northwestern border of Guatemala. To the west, much of the state lies in the Gulf Coastal Plain, where it merges with part of this physiographic region in Veracruz, and to the east, this plain merges with the lowlands of the Yucatan Peninsula. The two principal portions of the state are connected by a slender segment of land at least 6 km in width between Campeche and Chiapas, through which passes a portion of the Usumacinta River (Google Earth, https://earth.google.com, accessed: 9 May 2022).

The hydrography of Tabasco is dominated by the presence of portions of the first and second largest watersheds in Mexico, those of the Grijalva and the Usumacinta rivers, which arise from divergent points in the central highlands of Chiapas (the Grijalva) and the central highlands of Guatemala (Usumacinta) and join together in a common delta before entering the Gulf of Mexico near the town of Frontera.

Tabasco is partitioned into 17 municipalities and its capital is Villahermosa. As of 2020, its population was 2,402,598, which ranks 20th in the country. More recently its density was noted as 97 people/km^2, ranking 12th in the country (http://inegi.org; accessed 5 May 2022). This figure is 1.6 times the average density for Mexico.

The southeasternmost portion of the state contains the highest elevation (http://inegi.org; accessed 5 May 2022), between 1,140 and 1,150 m on an unnamed peak located at 17°24'38"N, 92°50'22"W near the border with Chiapas, more or less south of Villahermosa (http://peakbagger.com; accessed 7 June 2021). As expected, the lowest elevation in the state is sea level, all along the 198.8 km of shoreline (http://inegi.org; accessed 5 May 2022).

Materials and Methods

Our Taxonomic Position

In this paper we follow the same taxonomic position as detailed in previous works on other portions of Mesoamerica (Johnson et al. 2015a,b; Mata-Silva et al. 2015; Terán-Juárez et al. 2016; Woolrich-Piña et al. 2016, 2017; Nevárez-de los Reyes et al. 2016; Cruz-Sáenz et al. 2017; Gonzalez-Sánchez et al. 2017; Lazcano et al. 2019; Ramírez-Bautista et al. 2020; Torres-Hernández et al. 2021; Cruz-Elizalde et al. 2022). Johnson (2015a) can be consulted for a formal statement of this position, with special reference to the subspecies concept.

System for Determining Distributional Status

We employed the same system developed by Alvarado-Díaz et al. (2013) for the herpetofauna of Michoacán to ascertain the distributional status of members of the herpetofauna of Tabasco. Subsequently, Mata-Silva et al. (2015), Johnson et al. (2015a), Terán-Juárez et al. (2016), Woolrich-Piña et al. (2016, 2017), Nevárez-de los Reyes et al. (2016), Cruz-Sánchez et al. (2017), González-Sánchez et al. (2017), Lazcano et al. (2019), Ramírez-Bautista et al. (2020), Torres-Hernández et al. (2021), and Cruz-Elizalde et al. (2022) utilized this system, which consists of four categories: SE = endemic to Tabasco; CE = endemic to Mexico; NE = not endemic to Mexico; and NN = non-native in Mexico.

Systems for Determining Conservation Status

To assess the conservation status of the herpetofauna of Tabasco, we employed the same three systems (i.e., SEMARNAT, IUCN, and EVS) used by Alvarado-Díaz et al. (2013), Mata-Silva et al. (2015), Johnson et al. (2015a), Terán-Juárez et al. (2016), Woolrich-Piña et al. (2016, 2017), Nevárez-de los Reyes et al. (2016), Cruz-Sánchez et al. (2017), González-Sánchez et al. (2017), Lazcano et al. (2019), Ramírez-Bautista et al. (2020), Torres-Hernández et al. (2021), and Cruz-Elizalde et al. (2022). Detailed descriptions of these three systems appear in the earlier papers of this series, and thus are not repeated here.

The Mexican Conservation Series

The Mexican Conservation Series (MCS) was initiated in 2013, with a study of the herpetofauna of Michoacán (Alvarado-Díaz et al. 2013), as a part of a set of five papers designated as the "Special Mexico Issue" published in *Amphibian & Reptile Conservation*. The basic format of the entries in the MCS was established in this paper, i.e., providing an examination of the composition, physiographic distribution, and conservation status of the herpetofauna of a given Mexican state or group of states. Two years later, the MCS resumed with a paper on the herpetofauna of Oaxaca (Mata-Silva et al. 2015). That same year, Johnson et al. (2015a) presented a paper on the herpetofauna of Chiapas. The following year, three entries in the MCS appeared, on Tamaulipas (Terán-Juárez et al. 2016), Nayarit (Woolrich-Piña et al. 2016), and Nuevo León (Nevárez-de los Reyes et al. 2016). Thereafter, three entries were published in 2017, on Jalisco (Cruz-Sáenz et al. 2017), the Mexican Yucatan Peninsula (González-Sánchez et al. 2017), and Puebla (Woolrich-Piña et al. 2017), followed by subsequent entries on Coahuila (Lazcano et al. 2019), Hidaldo (Ramírez-Bautista et al. 2020), Veracruz (Torres-Hernández et al. 2021), and most recently one on Querétaro (Cruz-Elizalde et al. 2022). Therefore, this paper on the herpetofauna of Tabasco is number 14 in this series.

Physiography and Climate

Physiographic Regions

To analyze the distribution of the herpetofauna of Tabasco, we used the classification system of physiographic regions of INEGI (1986 and 2016). According to these studies, two physiographic regions are distinguished, one with two subregions (Fig. 1), which are described here.

Gulf Coastal Plain (GCP). This province (Fig. 2) comprises 95.7% of the state's area. Located in southeastern Mexico, it encompasses the states of Campeche, Chiapas, Oaxaca, Tabasco, and Veracruz; and its average length in each state is between 125 and 150 km. To the north, its limits are defined by the Gulf of Mexico; to the east, by the Yucatan Peninsula and Belize; to the south, by the Central American Cordillera and the Sierras de Chiapas and Oaxaca; and to the west by the Sierra Madre del Sur and Sierra Volcánica Transversal or Eje Neovolcánico.

The Gulf Coastal Plain was formed by alluvium carried by the Papaloapan, Coatzacoalcos, Grijalva, and Usumacinta rivers, which cross the province before emptying into the Gulf of Mexico. In the central part of this plain, the lower basins of the Grijalva and Usumacinta rivers (the largest basins in the country) meet and then converge south of the port of Frontera, Tabasco, to exit into the Gulf of Mexico. The Usumacinta

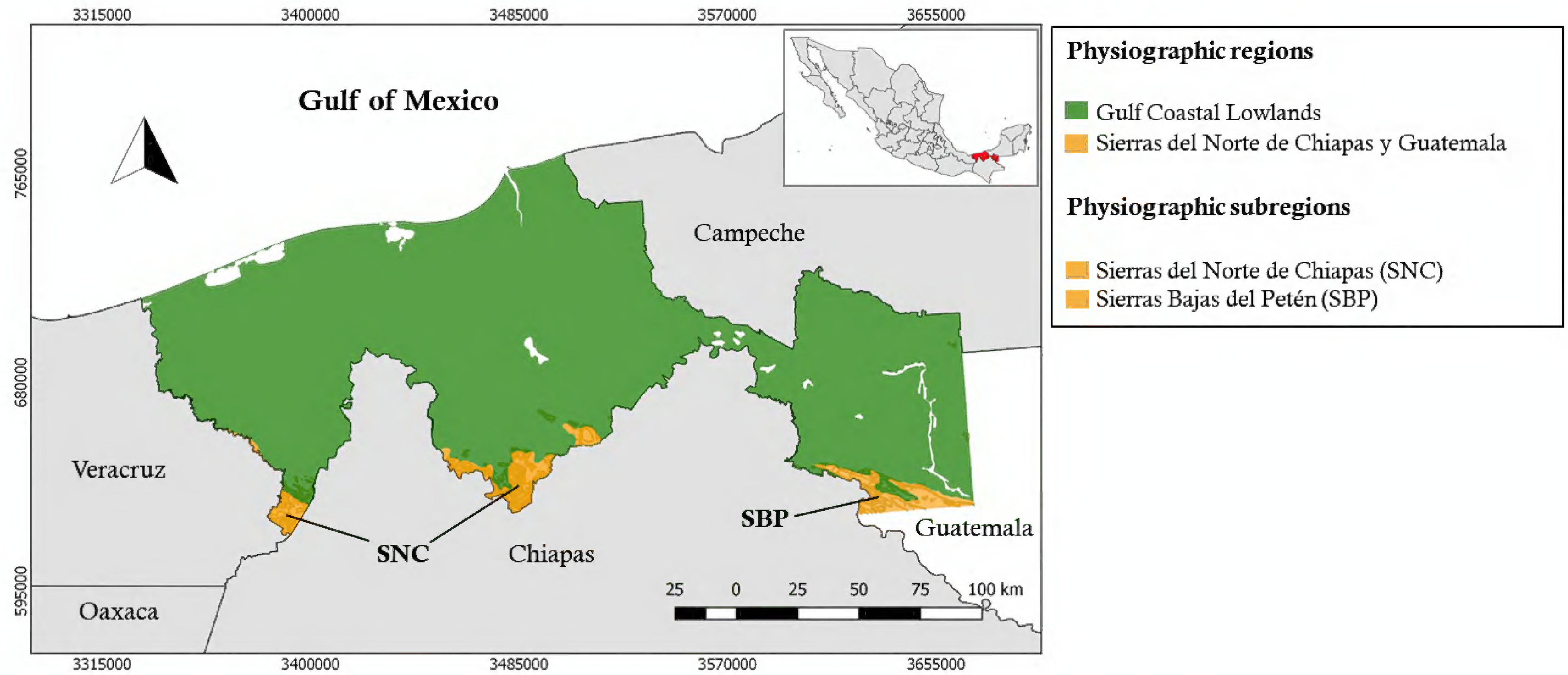

Fig. 1. Physiographic regions in the state of Tabasco, Mexico, and location of the state in Mexico.

and Grijalva rivers contribute about 27% of Mexico's hydrologic resources (West et al. 1985). Throughout most of this province, relatively young sedimentary rocks form extensive alluvial plains and coastal plains with an almost flat relief at elevations below 100 m. This relief creates extensive flood plains and lagoons, among which La Machona, Mecoacán, Sitio Grande, and El Rosario are the most prominent (INEGI 2006; SAHOP 1980). Two types of climates are evident: (i) warm humid with abundant rainfall in summer, which covers 76.0% of the surface area and is distributed from the coastal zone to the vicinity of the mountains in the southern portion of the state, and (ii) warm subhumid with summer rains, which is present toward northeastern Tabasco, in the municipality of Balancán. This region is the least humid in the state, with an average annual temperature of 26.4 °C (INEGI 2016).

Grasslands used for grazing livestock have displaced the natural vegetation in this physiographic region, as they cover 30.6% of the area; and additional agricultural areas occupy 25.8% of this region. The third most common type of vegetation is the Tular-popal association, which forms dense patches that cover 26.6% of the swampy areas. In addition, some forests are dominated by a single species (16.2%), such as Cashan (*Terminalia amazonia*), laurel (*Nectandra* sp.), Mulato (*Bursera simaruba*) or Chicozapote (*Achras zapota*). To a lesser degree, the mangroves (2.8%), which are composed of a group of halophilic plants, are characterized by such dominant species as Red Mangrove (*Rhizophora mangle*), Black Mangrove (*Avicennia germinans*), or White Mangrove (*Laguncularia racemosa*) (INEGI 2016).

Sierras Bajas del Petén (SBP). This province (Fig. 3) only covers 4.3% of the area of the state, and includes the mountains that extend from southeastern Mexico to Guatemala. This region is characterized by a parallel arrangement of folded mountain ranges with rounded summits, steep flanks, and wide intermontane valleys at its base (Zavala-Cruz and Ortiz-Pérez 2019). To the north, this province is limited by the occurrence of the Gulf Coastal Plain, to the east by Belize, to the south by Guatemala, and to the west it borders the Central American Mountain Cordillera. This province is divided into five physiographic subprovinces, two of which occur in Tabasco: the northern Sierras of Chiapas and the Lower Sierras of Petén.

Sierras del Norte de Chiapas (SNC). In Tabasco, this region (Fig. 4) is composed of two small portions to the south that together cover an area of 986.0 km² and comprise parts of the municipalities of Huimanguillo, Macuspana, Tacotalpa, and Teapa (INEGI 1986). In these areas, the highest elevations are the hills of La Pava and La Ventana (at elevations of 880 and 560 m, respectively); and the Madrigal, Tapijulapa, and Poana Mountains (at elevations from 560 to 900 m). The lower hills are La Campana, La Corona, Coconá, Mono Pelado, and El Tortuguero (CONAFOR 2013). Limestone rocks such as dolomites and marls dominate this region, and they alternate with shales and sandstones, but there also are many types of ancient alluvium, igneous rocks formed from volcanic clasts, andesites, and volcanic ash. The lithological diversity gives these mountain ranges a "complex character" (INEGI 1989; Zavala-Cruz and Ortiz-Pérez 2019), and karst features are prominent.

Climate

Temperature. Here, we present the monthly minimum, mean, and maximum temperatures for a single locality in each of the three recognized physiographic regions in Tabasco (Table 1). The elevations for these three localities range from 10 m at Villahermosa in the Gulf

Fig. 2. Gulf Coastal Plain. Mangroves in the municipality Paraíso, Tabasco. *Photo by José del Carmen Gerónimo-Torres.*

Fig. 3. Sierras Bajas del Petén. Panoramic view of the Sierras Bajas del Petén, Ejido Nuevo Progreso, municipality of Tenosique, Tabasco, near the border with Guatemala. *Photo by Nelly del Carmen Jiménez-Pérez.*

Fig. 4. Sierra Norte de Chiapas. Mountain Cloud Forest fragment in the municipality of Huimanguillo, Tabasco. *Photo by Liliana Ríos-Rodas.*

Coastal Plain to 34 m at Huimanguillo in the Sierra Norte de Chiapas.

The mean annual temperature (MAT) is highest at Tenosique (elevation 19 m) in the Sierras Bajas del Petén (SBP) at 26.7 °C. The MAT for the other two localities in the Gulf Coastal Plain (GCP) and the Sierra Norte de Chiapas (SNC) differ by only 0.1 °C (26.4 °C for the GCP and 26.3 °C for the SNC). These values are reflective of the limited variation in elevational range in Tabasco.

The minimum annual temperatures range from 21.6 °C in the SBP and the SNC to 23 °C in the GCP, which only represents a difference of 1.4 °C (Table 1). The mean minimum monthly temperatures peak in May in the GCP and SBP (at 25.6 °C in the former, and 23.6 °C in the latter) and in June in the SNC (at 23.7 °C). The mean maximum monthly temperatures are highest in May in all three regions, respectively 34.8 °C, 35 °C, and 35.4 °C in the GLC, SNC, and SBP. The monthly maximum temperatures are lowest in January in the GCP (at 26.7 °C) and SBP (at 28.0 °C), and in December and January in the SNC (at 26.9 °C).

Precipitation. Naturally, monthly precipitation is lowest during the dry season in February (in the SBP), March (in the GCP), or April (in the SNC), and highest during the rainy season in September in all three regions (Table 2). The data in Table 2 demonstrate that 63.0–76.3% of the yearly precipitation falls during the rainy season, from May to October. The annual rainfall ranges from 1,476.0 mm in the SBP to 2,316.8 mm in the SNC (Table 2).

Composition of the Herpetofauna

Families

The members of the native and non-native herpetofauna of Tabasco are arranged among 45 families, including 10 families of anurans, one of salamanders, one of caecilians, one of crocodylians, 24 of squamates, and eight of turtles (Table 3). The total of 45 families includes 72.6% of the 62 families with native, non-native, and introduced/questionable members represented in Mexico (J. Johnson, unpublished, 26 March 2022). Among the 12 amphibian families, 51.1% of the species (Tables 4 and 5) are classified in the families Craugastoridae (seven species) and Hylidae (16 species). Among the 33 reptile families, 59.5% of the species (Tables 4 and 5) are classified in the families Dactyloidae (14 species), Phrynosomatidae (five), Colubridae (20), Dipsadidae (30), and Viperidae (six).

Genera

The genera of amphibians and reptiles represented in Tabasco number 104, including 24 genera of anurans, one of salamanders, one of caecilians, one of crocodylians, 67 of squamates, and 10 of turtles. These 104 genera include 48.8% of the 213 recorded for Mexico (J. Johnson, unpublished, 26 March 2022). Among the amphibians (Table 4), the largest numbers of species are classified in the genera *Craugastor* (seven species) and *Bolitoglossa* (five); among the reptiles (Table 4), the most speciose genera are *Norops* (14 species), *Sceloporus* (five), and *Coniophanes* (six).

Species

The herpetofauna of Tabasco consists of 170 species, including 39 anurans, five salamanders, one caecilian, two crocodylians, 111 squamates, and 12 turtles (Tables 3

Table 1. Monthly minimum (Min), mean (Mean, in parentheses), maximum (Max), and annual temperature data (in °C) for the three physiographic regions of Tabasco, Mexico. The selected localities for each region and their elevations are as follows: Gulf Coastal Plain—Cárdenas (29 m asl), Centla (4 m), Villahermosa (10 m); Sierra Norte de Chiapas—Huimanguillo (29 m), Teapa (41 m), Macuspana (13 m); and Sierras Bajas del Petén—Tenosique (19 m). Data were taken from https://es.climate-data.org and https://smn.conagua.gob.mx/es/climatologia (Accessed: 16 June 2021).

Physiographic region	January	February	March	April	May	June	July	August	September	October	November	December	Annual
Gulf Coastal Plain	20.1 (22.8) 26.5	21.0 (24.1) 28.4	22.4 (26.2) 31.2	24.4 (28.6) 33.9	25.8 (29.5) 34.3	25.2 (28.1) 32.1	25.2 (28.4) 32.5	25.2 (28.1) 32.1	24.5 (26.9) 30.5	23.6 (25.9) 29.1	21.9 (24.4) 27.7	20.8 (23.5) 27.0	23.3 (26.4) 30.4
Sierra Norte de Chiapas	18.3 (22.2) 26.5	19.0 (23.4) 28.1	20.2 (25.3) 30.9	22.2 (27.7) 33.4	23.7 (28.9) 34.3	23.7 (28.1) 32.8	23.3 (27.8) 32.6	23.3 (27.6) 32.2	23.1 (26.8) 31.0	22.1 (25.6) 29.5	20.3 (24.0) 28.0	19.1 (22.8) 26.9	21.5 (25.8) 30.5
Sierras Bajas del Petén	18.8 (23.4) 28	19.4 (24.6) 29.7	20.4 (26.3) 32.1	22.5 (28.6) 34.8	23.6 (29.5) 35.4	23.5 (28.6) 33.7	22.9 (28) 33.1	22.9 (28.2) 33.5	22.9 (27.8) 32.7	22.3 (26.7) 31.2	20.7 (25.2) 29.8	19.4 (23.9) 28.5	21.6 (26.7) 31.9

and 4). The current numbers of native species in Mexico for these six groups are, respectively, 258, 155, 3, 3, 902, and 51 (J. Johnson, unpublished, 26 March 2022). The 165 native species in Tabasco comprise 12.0% of the 1,372 species in the entire native Mexican herpetofauna (J. Johnson, unpublished, 29 May 2021).

Three states in Mexico border Tabasco, and all have been evaluated in the Mexican Conservation Series (Chiapas: Johnson et al. 2015a; Campeche: González-Sánchez et al. 2017; Veracruz: Torres-Hernández et al. 2021). Based on these works, the total figures for the native taxa in these states are as follows: Chiapas, 326; Campeche, 125; and Veracruz, 351. The number of native species in Tabasco (165) is closest to that in Campeche, essentially another lowland state in the western portion of the Yucatan Peninsula. As expected, the two larger and more montane states to the north (Veracruz) and south (Chiapas) contain 2.1 and 2.0 times as many species, respectively, as Tabasco.

Patterns of Physiographic Distribution

We used a system of three regions (Fig. 1) to analyze the physiographic distribution patterns of members of the Tabasco herpetofauna. The results for the 170 species are tabulated in Table 4 and summarized in Table 5.

The total number of taxa in each of the three regions we recognize ranges from 88 in the Gulf Coastal Plain to 145 in the Sierra Norte de Chiapas. The total for the remaining area (Sierras Bajas del Petén) is 93. The average of these three values is 108.7, or 63.9% of the number for the total herpetofauna (170). The lowest value (88) is 51.8% of the total value (170), and the corresponding percentages for the other two regions in numerical order are 54.7 (93/170) and 85.3 (145/170). These results indicate that the higher elevations in the state, as in the Sierra Norte de Chiapas (see above), exhibit much greater herpetofaunal diversity than the corresponding lower elevations. This situation is consistent with the recognition that herpetofaunal diversity in Mexico is highest in the nearby or bordering states of Oaxaca and Chiapas (Mata-Silva et al. 2015; Johnson et al. 2015a) to the south.

Six herpetofaunal groups are represented in Tabasco, i.e., anurans, salamanders, caecilians, crocodylians, squamates, and turtles. As is typical for the state herpetofaunas in Mexico, anurans and squamates contain the largest numbers of species and the caecilians and crocodylians the fewest, while the salamanders and turtles are represented by intermediate numbers. The largest numbers of anurans (36 of 39, or 92.3%), salamanders (four of five, or 80.0%), and squamates (96 of 111, or 86.5%) and of the herpetofauna in general (145 of 170, or 85.4%) occupy the Sierra Norte de Chiapas. Nonetheless, turtles do not follow this pattern, inasmuch as all 12 of the species in Tabasco occur on the Gulf Coastal Plain, with only six of them (50.0%) occurring in the Sierra Norte de Chiapas, and

No. 1. *Hyalinobatrachium viridissimum* (Taylor, 1942). The Northern Glassfrog is a non-endemic species distributed from Guerrero and Veracruz, Mexico, through Guatemala and Belize to northwestern Honduras, and possibly to the departments of Santa Ana and Cabañas in El Salvador (https://amphibiansoftheworld.amnh.org/). This individual is from Muku Chem, in the municipality of Tacotalpa, Tabasco. Torres-Hernández et al. (2021) calculated its EVS as 11, placing it in the lower portion of the medium vulnerability category. Its conservation status has not been assessed by either the IUCN or SEMARNAT. *Photo by Manuel Hernández-May.*

No. 2. *Craugastor alfredi* (Boulenger, 1898). Alfred's Rain Frog is distributed from central Veracruz, northern Oaxaca, and southward to the states of Tabasco and Chiapas, Mexico (https://amphibiansoftheworld.amnh.org/). This individual was located at Muku Chem, in the municipality of Tacotalpa, Tabasco. Wilson et al. (2013b) determined its EVS as 9, placing it at the upper limit of the low vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN, but this species is not listed by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

No. 3. *Craugastor berkenbuschii* (Peters, 1870). Berkenbusch's Robber Frog ranges along the Atlantic slopes of southern San Luis Potosí, Hidalgo, Puebla, Veracruz, Tabasco, and northern Oaxaca, north of the Isthmus of Tehuantepec, Mexico (https://amphibiansoftheworld.amnh.org/). This individual was located at Muku Chem, in the municipality of Tacotalpa, Tabasco. Wilson et al. (2013b) assessed its EVS as 14, placing it at the lower limit of the high vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN and as a species of Special Protection (Pr) by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

No. 4. *Duellmanohyla chamulae* (Duellman, 1961). The Chamula Mountain Brook Frog is known only from a few localities at elevations above 1,600 m on the northern slopes of the Central Highlands of Chiapas and into adjacent extreme southwestern Tabasco, Mexico (https://amphibiansoftheworld.amnh.org/). This individual was encountered at Ejido Villa Guadalupe, in the municipality of Huimanguillo, Tabasco. Wilson et al. (2013b) determined its EVS to be 13, placing it at the upper limit of the medium vulnerability category. Its conservation status has been evaluated as Endangered (EN) by IUCN, and as a species of Special Protection (Pr) by SEMARNAT. *Photo by José del Carmen Gerónimo-Torres.*

Table 2. Monthly and annual precipitation data (in mm) for the three physiographic regions of Tabasco, Mexico. The selected localities for each of the regions, with elevation given in parentheses) are as follows: Gulf Coastal Plain—Cárdenas (29 m asl), Centla (4 m), Villahermosa (10 m); Sierra Norte de Chiapas—Huimanguillo (29 m), Teapa (41 m), Macuspana (13 m); Sierras Bajas del Petén—Tenosique (19 m). Data were taken from https://es.climate-data.org and https://smn.conagua.gob.mx/es/climatologia (Accessed: 16 June 2021). The shaded area indicates the months of the rainy season.

Physiographic region	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Annual
Gulf Coastal Plain	76.8	48.5	30.3	35.3	68.5	192.3	136.5	193.3	270.5	232.5	125.8	79.8	1,489.8
Sierra del Norte de Chiapas	172.5	140	82.5	74	120	257.3	193.8	247.8	341.5	299	210.3	178.3	2,316.8
Sierras Bajas del Petén	62	34	36	54	95	227	141	206	261	196	104	60	1,476

an intermediate number of nine (75.0%) occurs in the Selvas Bajas del Petén.

The members of the Tabasco herpetofauna are distributed in either one, two, or three physiographic regions (Table 4), as follows: one (69 of 170 species; 40.6%); two (46; 27.1%); and three (55, 32.4%). The mean regional occupancy figure is 1.9, which is slightly higher than the 1.6 value for Querétaro, another state with three physiographic regions that was assessed in the Mexican Conservation Series (Cruz-Elizalde et al. 2022). A sizable portion of the 170 species in Tabasco (115; 67.6%) occurs in only one or two of the three physiographic regions, which is of considerable conservation significance (see below).

The number of species occupying a single physiographic region ranges from eight in the Sierras Bajas del Petén (SBP) to 50 in the Sierra Norte de Chiapas (SNC).

The 50 single-region species in the SNC (Table 7) are as follows (numbers refer to distributional categories as reported by Wilson et al. [2017], and asterisks indicate the country endemics):

Incilius macrocristatus 4
Hyalinobatrachium viridissimum 4
*Craugastor berkenbuschii**
*Craugastor pelorus**
*Charadrahyla chaneque**
*Duellmanohyla chamulae**
*Exerodonta bivocata**
Ptychohyla macrotympanum 4
*Quilticohyla zoque**
*Rheohyla miotympanum**
Triprion spinosus 4
Gastrophryne elegans 4
Agalychnis moreletii 4
*Bolitoglossa platydactyla**
Bolitoglossa rufescens 4
*Bolitoglossa veracrucis**
*Norops barkeri**
Norops capito 4
*Norops compressicauda**
Norops laeviventris 4
Norops petersi 4
*Lepidophyma tuxtlae**
Xenosaurus rackhami 4
Dendrophidion vinitor 4
Ficimia publia 4
Phrynonax poecilonotus 6
Senticolis triaspis 7
Stenorrhina freminvillii 4
Tantilla rubra 4
Tantilla schistosa 4
Tantillita lintoni 4
Adelphicos quadrivirgatum 4
Amastridium sapperi 4
Coniophanes piceivittis 4
Dipsas brevifacies 4
Geophis carinosus 4
*Geophis laticinctus**
Geophis sanniolus 4
Leptodeira maculata 4
Leptodeira septentrionalis 4
Ninia diademata 4
Oxyrhopus petolarius 6
Rhadinaea decorata 6
Sibon dimidiatus 4
Sibon nebulatus 6
Xenodon rabdocephalus 6
Micrurus elegans 4
Scaphiodontophis annulatus 4
Amerotyphlops tenuis 4
Bothriechis schlegelii 6

Table 3. Taxonomic composition of the native and non-native herpetofauna of Tabasco, Mexico.

Order	Families	Genera	Species
Anura	10	24	39
Caudata	1	1	5
Gymnophiona	1	1	1
Subtotal	**12**	**26**	**45**
Crocodylia	1	1	2
Squamata	24	67	111
Testudines	8	10	12
Subtotal	**33**	**78**	**125**
Total	**45**	**104**	**170**

No. 5. *Exerodonta bivocata* (Duellman and Hoyt, 1961). The Chiapan Highlands Treefrog is distributed along the Atlantic slopes of extreme southwestern Tabasco, Oaxaca, and Chiapas in southern Mexico (https://amphibiansoftheworld.amnh.org/). This individual was located in Ejido Villa Guadalupe, in the municipality of Huimanguillo, Tabasco. Wilson et al. (2013b) assessed its EVS as 15, placing it in the lower portion of the high vulnerability category. Its conservation status has been judged as Endangered (EN) by the IUCN, but this species is not listed by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

No. 6. *Ptychohyla macrotympanum* (Tanner, 1957). The Pine Forest Stream Frog is distributed in humid montane and pine-oak forest, on the northern slopes of the Chiapan Highlands of Tabasco and Chiapas in Mexico (https://amphibiansoftheworld.amnh.org/). This individual was found in the Ejido Villa Guadalupe of Huimanguillo, Tabasco. Wilson et al. (2013b) assessed its EVS as 11, placing it in the lower portion of the medium vulnerability category. Its conservation status has been considered as Vulnerable (VU) by the IUCN, but this species is not listed by SEMARNAT. *Photo by Jenny del Carmen Estrada-Montiel.*

No. 7. *Quilticohyla zoque* (Canseco-Márquez, Aguilar-López, Luría-Manzano, Pineda-Arredondo, and Caviedes-Solis, 2017). The Zoque Treefrog is distributed in evergreen tropical forest at three localities in southern Mexico in the Selva Zoque, two in southern Veracruz (Paso del Moral and Arroyo Zarco), one in extreme southwestern Tabasco near the Veracruz and Chiapas borders, and one in northeastern Oaxaca (Chalchijapa) (https://amphibiansoftheworld.amnh.org/). This individual was located in Ejido Villa Guadalupe, in the municipality of Huimanguillo, Tabasco. Torres-Hernández et al. (2021) assessed its EVS as 14, placing it at the lower limit of the high vulnerability category. Its conservation status has been judged as Endangered (EN) by the IUCN, but this species is not listed by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

No. 8. *Triprion spinosus* (Steindachner, 1864). The Coronated Treefrog occurs in humid forests, primarily in the premontane zone of eastern Mexico in the states of Tabasco, Veracruz, Puebla, Oaxaca, and Chiapas, and on into Central America south into Panama (https://amphibiansoftheworld.amnh.org/). This individual is from Cerro El Madrigal, in the municipality of Teapa, Tabasco. Wilson et al. (2013b) calculated its EVS as 10, placing it in the lower portion of the medium vulnerability category. Its conservation status has been considered as Near Threatened (NT) by IUCN, but this species is not listed by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

Table 4. Distribution of the herpetofauna of Tabasco, Mexico, by physiographic region. No asterisk = non-endemic; * = country endemic; ** = non-native.

Taxon	Physiographic region			Number of regions
	Gulf Coastal Plain (GCP)	Sierras de Chiapas y Guatemala		
		Sierra del Norte de Chiapas (SNC)	Sierras Bajas del Petén (SBP)	
Total herpetofauna (170 species)				
AMPHIBIA (45 species)				
Anura (39 species)				
Bufonidae (3 species)				
Incilius macrocristatus		+		1
Incilius valliceps	+	+	+	3
Rhinella horribilis	+	+	+	3
Centrolenidae (1 species)				
Hyalinobatrachium viridissimum		+		1
Craugastoridae (7 species)				
Craugastor alfredi		+	+	2
*Craugastor berkenbuschii**		+		1
Craugastor laticeps		+	+	2
Craugastor loki		+	+	2
Craugastor palenque		+	+	2
*Craugastor pelorus**		+		1
*Craugastor rhodopis**	+	+	+	3
Eleutherodactylidae (2 species)				
Eleutherodactylus leprus		+	+	2
*Eleutherodactylus planirostris***	+			1
Hylidae (16 species)				
*Charadrahyla chaneque**		+		1
Dendrosophus ebraccatus	+	+		2
Dendrosophus microcephalus	+	+	+	3
*Duellmanohyla chamulae**		+		1
*Exerodonta bivocata**		+		1
Ptychohyla macrotympanum		+		1
*Quilticohyla zoque**		+		1
*Rheohyla miotympanum**		+		1
Scinax staufferi	+	+	+	3
Smilisca baudinii	+	+	+	3
Smilisca cyanosticta		+	+	2
Tlalocohyla loquax	+	+	+	3
Tlalocohyla picta	+	+		2
Trachycephalus vermiculatus	+	+	+	3
Triprion petasatus			+	1
Triprion spinosus		+		1
Leptodactylidae (3 species)				
Engystomops pustulosus			+	1
Leptodactylus fragilis	+	+		2
Leptodactylus melanonotus	+	+	+	3
Microhylidae (2 species)				
Gastrophyrne elegans		+		1
Hypopachus variolosus		+	+	2
Phyllomedusidae (2 species)				
Agalychnis moreletii		+		1
Agalychnis taylori	+	+	+	3
Ranidae (2 species)				
Lithobates brownorum	+	+	+	3

Table 4 (continued). Distribution of the herpetofauna of Tabasco, Mexico, by physiographic region. No asterisk = non-endemic; * = country endemic; ** = non-native.

Taxon	Physiographic region			Number of regions
	Gulf Coastal Plain (GCP)	Sierras de Chiapas y Guatemala		
		Sierra del Norte de Chiapas (SNC)	Sierras Bajas del Petén (SBP)	
Lithobates vaillanti	+	+	+	3
Rhinophrynidae (1 species)				
Rhinophrynus dorsalis	+	+	+	3
Caudata (5 species)				
Plethodontidae (5 species)				
*Bolitoglossa alberchi**			+	1
Bolitoglossa mexicana	+	+	+	3
*Bolitoglossa platydactyla**		+		1
Bolitoglossa rufescens		+		1
*Bolitoglossa veracrucis**		+		1
Gymnophiona (1 species)				
Dermophiidae (1 species)				
Dermophis mexicanus	+	+	+	3
Reptilia (125 species)				
Crocodylia (2 species)				
Crocodylidae (2 Species)				
Crocodylus acutus	+	+	+	3
Crocodylus moreletii	+	+	+	3
Squamata (111 species)				
Corytophanidae (4 species)				
Basiliscus vittatus	+	+	+	3
Corytophanes cristatus		+	+	2
Corytophanes hernandezii		+	+	2
Laemanctus longipes		+	+	2
Dactyloidae (14 species)				
*Norops barkeri**		+		1
Norops beckeri	+	+	+	3
Norops biporcatus	+	+	+	3
Norops capito		+		1
*Norops compressicauda**		+		1
Norops laeviventris		+		1
Norops lemurinus	+	+	+	3
Norops petersii		+		1
Norops rodriguezii	+	+	+	3
*Norops sagrei***	+	+	+	3
Norops sericeus	+	+	+	3
Norops tropidonotus	+	+	+	3
Norops uniformis	+	+	+	3
Norops unilobatus		+	+	2
Diploglossidae (1 species)				
Celestus rozellae		+	+	2
Eublepharidae (1 species)				
Coleonyx elegans		+	+	2
Gekkonidae (2 species)				
*Hemidactylus frenatus***	+	+	+	3
*Hemidactylus turcicus***	+	+		2
Iguanidae (2 species)				
Ctenosaura similis	+	+	+	3

Table 4 (continued). Distribution of the herpetofauna of Tabasco, Mexico, by physiographic region. No asterisk = non-endemic; * = country endemic; ** = non-native.

Taxon	Physiographic region			Number of regions
	Gulf Coastal Plain (GCP)	Sierras de Chiapas y Guatemala		
		Sierra del Norte de Chiapas (SNC)	Sierras Bajas del Petén (SBP)	
Iguana rhinolopha	+	+	+	3
Mabuyidae (1 species)				
Marisora lineola	+	+		2
Phrynosomatidae (5 species)				
Sceloporus chrysostictus	+	+	+	3
Sceloporus lundelli		+	+	2
Sceloporus serrifer		+	+	2
Sceloporus teapensis	+	+	+	3
Sceloporus variabilis	+	+	+	3
Phyllodactylidae (1 species)				
Thecadactylus rapicauda		+	+	2
Scincidae (2 species)				
Mesoscincus schwartzei	+		+	2
Plestiodon sumichrasti	+	+		2
Sphaerodactylidae (2 species)				
Sphaerodactylus continentalis		+	+	2
Sphaerodactylus glaucus	+	+	+	3
Sphenomorphidae (2 species)				
Scincella cherriei	+	+	+	3
*Scincella gemmingeri**			+	1
Teiidae (5 species)				
Aspidoscelis deppii	+	+	+	3
*Aspidoscelis guttatus**	+			1
*Holcosus amphigrammus**	+	+		2
Holcosus festivus	+	+	+	3
*Holcosus stuarti**	+	+		2
Xantusiidae (2 species)				
Lepidophyma flavimaculatum		+	+	2
*Lepidophyma tuxtlae**		+		1
Xenosauridae (1 species)				
Xenosaurus rackhami		+		1
Boidae (1 species)				
Boa imperator	+	+	+	3
Colubridae (20 species)				
Dendrophidion vinitor		+		1
Drymarchon melanurus	+	+	+	3
Drymobius margaritiferus	+	+	+	3
Ficimia publia		+		1
Lampropeltis polyzona	+	+		2
Leptophis ahaetulla		+	+	2
Leptophis mexicanus	+	+	+	3
Masticophis mentovarius	+	+	+	3
Mastigodryas melanolomus	+	+		2
Oxybelis fulgidus	+			1
Oxybelis potosiensis	+	+	+	3
Phrynonax poecilonotus		+		1
Pseudelaphe flavirufa		+	+	2
Senticolis triaspis		+		1
Spilotes pullatus	+	+	+	3

Table 4 (continued). Distribution of the herpetofauna of Tabasco, Mexico, by physiographic region. No asterisk = non-endemic; * = country endemic; ** = non-native.

Taxon	Physiographic region			Number of regions
	Gulf Coastal Plain (GCP)	Sierras de Chiapas y Guatemala		
		Sierra del Norte de Chiapas (SNC)	Sierras Bajas del Petén (SBP)	
Stenorrhina degenhardtii	+			1
Stenorrhina freminvillii		+		1
Tantilla rubra		+		1
Tantilla schistosa		+		1
Tantillita lintoni		+		1
Dipsadidae (30 species)				
Adelphicos quadrivirgatum		+		1
Amastridium sapperi		+		1
Clelia scytalina	+	+		2
Coniophanes bipunctatus	+	+		2
Coniophanes fissidens		+	+	2
Coniophanes imperialis	+	+	+	3
Coniophanes piceivittis		+		1
Coniophanes quinquevittatus	+	+	+	3
Coniophanes schmidti			+	1
Conophis lineatus	+		+	2
Dipsas brevifacies		+		1
Enulius flavitorques	+			1
Geophis carinosus		+		1
*Geophis laticinctus**		+		1
Geophis sanniolus		+		1
Geophis sartorii	+	+	+	3
Imantodes cenchoa	+	+	+	3
Imantodes gemmistratus		+	+	2
Leptodeira frenata			+	1
Leptodeira maculata		+		1
Leptodeira septentrionalis		+		1
Ninia diademata		+		1
Ninia sebae	+	+	+	3
Oxyrhopus petolarius		+		1
Pliocercus elapoides	+	+		2
Rhadinaea decorata		+		1
Sibon dimidiatus		+		1
Sibon nebulatus		+		1
Tretanorhinus nigroluteus	+	+		2
Xenodon rabdocephalus		+		1
Elapidae (2 species)				
*Micrurus diastema**	+	+		2
Micrurus elegans		+		1
Leptotyphlopidae (1 species)				
Epictia phenops	+			1
Natricidae (3 species)				
Nerodia rhombifera	+			1
Thamnophis marcianus	+		+	2
Thamnophis proximus	+	+		2
Sibynophiidae (1 species)				
Scaphiodontophis annulatus		+		1
Typhlopidae (2 species)				
Amerotyphlops tenuis		+		1

Table 4 (continued). Distribution of the herpetofauna of Tabasco, Mexico, by physiographic region. No asterisk = non-endemic; * = country endemic; ** = non-native.

Taxon	Physiographic region			Number of regions
	Gulf Coastal Plain (GCP)	Sierras de Chiapas y Guatemala		
		Sierra del Norte de Chiapas (SNC)	Sierras Bajas del Petén (SBP)	
*Virgotyphlops braminus***	+			1
Viperidae (6 species)				
Agkistrodon russeolus			+	1
Bothriechis schlegelii		+		1
Bothrops asper	+	+	+	3
Crotalus tzabcan			+	1
Metlapilcoatlus mexicanus		+	+	2
Porthidium nasutum		+	+	2
Testudines (12 species)				
Cheloniidae (2 species)				
Chelonia mydas	+			1
Lepidochelys kempii	+			1
Chelydridae (1 species)				
Chelydra rossignonii	+	+	+	3
Dermatemydidae (1 species)				
Dermatemys mawii	+	+	+	3
Dermochelyidae (1 species)				
Dermochelys coriacea	+			1
Emydidae (1 species)				
Trachemys venusta	+	+	+	3
Geoemydidae (1 species)				
Rhinoclemmys areolata	+		+	2
Kinosternidae (3 species)				
Kinosternon acutum	+	+	+	3
Kinosternon leucostomum	+	+	+	3
Kinosternon scorpioides	+		+	2
Staurotypidae (2 species)				
Claudius angustatus	+		+	2
Staurotypus triporcatus	+	+	+	3

Thirteen of these 50 species (26.0%) are country endemics and 37 (74.0%) are non-endemics. Thirty of the 37 non-endemics (81.1%) are MXCA species, and thus are distributed some distance from Mexico into Central America. Six of these non-endemics (16.2%) are MXSA species, and thus range from Mexico through Central America and into South America. Finally, one non-endemic (2.7%) is a USCA species, and thus ranges from the United States to Central America.

The 11 single-region species in the GCP (Table 7) are as follows (numbers refer to the distributional categories as designated by Wilson et al. [2017]; one asterisk indicates a country endemic species; and two asterisks a non-native species):

*Eleutherodactylus planirostris***
*Aspidoscelis guttatus**
Oxybelis fulgidus 6
Stenorrhina freminvillii 4
Enulius flavitorques 6
Epictia phenops 4
Nerodia rhombifera 3
*Virgotyphlops braminus***
Chelonia mydas 9
Lepidochelys kempii 9
Dermochelys coriacea 9

Note that only one of these 11 species (9.1%) is a country endemic, two (18.2%) are non-natives, and eight (72.7%) are non-endemics. Of the eight non-endemics, one is a MXUS species (12.5%), the only one in Tabasco that ranges northward from Mexico into the United States. Two of these are MXCA species (25.0%), two are MXSA species (25.0%), and three are OCEA (or oceanic) species (37.5%; the sea turtles).

No. 9. *Leptodactylus fragilis* (Brocchi, 1877). The White-lipped Frog is distributed from the Lower Rio Grande Valley of southern Texas (USA) through eastern and southern Mexico (southeast from Colima), and into Central America through northern and western Colombia (https://amphibiansoftheworld.amnh.org/). This individual was found in the Ejido Villa Guadalupe of Huimanguillo, Tabasco. Wilson et al. (2013b) calculated its EVS as 5, placing it in the lower portion of the low vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN, but this species is not listed by SEMARNAT. *Photo by José del Carmen Gerónimo-Torres.*

No. 10. *Agalychnis taylori* Funkhouser, 1957. Taylor's Leaf Frog occurs on the Atlantic slopes and lowlands from southern Veracruz and northern Oaxaca in Mexico, through the more humid portions of Tabasco, Campeche, Quintana Roo and Yucatan, and on through Guatemala to west-central Honduras (https://amphibiansoftheworld.amnh.org/). This individual was found in the municipality of Centro, Tabasco. Torres-Hernández et al. (2021) calculated its EVS as 11, placing it in the lower portion of the medium vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN, but this species is not listed by SEMARNAT. *Photo by José del Carmen Gerónimo-Torres.*

No. 11. *Lithobates vaillanti* (Brocchi, 1877). Vaillant's Frog ranges from "low and moderate elevations from north-central Veracruz and northern Oaxaca to the central Rio Magdalena region in Colombia on the Atlantic versant and on the Pacific versant in southeastern Oaxaca and northwestern Chiapas, Mexico, and from northwestern Nicaragua to southwestern Ecuador" (https://amphibiansoftheworld.amnh.org/). This individual was located in the Ejido Villa Guadalupe of Huimanguillo, Tabasco. Wilson et al. (2013b) determined its EVS as 9, placing it at the upper limit of the low vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN, but this species is not listed by SEMARNAT. *Photo by José del Carmen Gerónimo-Torres.*

No. 12. *Bolitoglossa mexicana* Duméril, Bibron, and Duméril, 1854. The Mexican Mushroom-tongued Salamander is distributed from the "Atlantic slope from southern Veracruz (Mexico) across the base of the Yucatan Peninsula, with an isolated population in the northern part of Yucatan Peninsula, to Honduras (extending to the Pacific versant in the Ocotepeque) and El Salvador (Departamento de Chalatenango, municipio de La Palma, Cerro La Palma)" (https://amphibiansoftheworld.amnh.org/). This individual was encountered in Villa Luz, in the municipality of Tacotalpa, Tabasco. Wilson et al. (2013b) assessed its EVS as 11, placing it in the lower portion of the medium vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN and it is allocated to the Special Protection (Pr) category by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

Table 5. Distribution of herpetofaunal families in Tabasco, Mexico, by physiographic province. See Table 4 header for an explanation of the abbreviations.

Family	Number of species	Distribution among physiographic regions		
		GCP	SNC	SBP
Bufonidae	3	2	3	2
Centrolenidae	1	—	1	—
Craugastoridae	7	1	7	5
Eleutherodactylidae	2	1	1	1
Hylidae	16	7	15	7
Leptodactylidae	3	2	2	2
Microhylidae	2	—	2	1
Phyllomedusidae	2	1	2	1
Ranidae	2	2	2	2
Rhinophrynidae	1	1	1	1
Subtotal	**39**	**17**	**36**	**22**
Plethodontidae	5	1	4	2
Subtotal	**5**	**1**	**4**	**2**
Dermophiidae	1	1	1	1
Subtotal	**1**	**1**	**1**	**1**
Total	**45**	**19**	**41**	**25**
Crocodylidae	2	2	2	2
Subtotal	**2**	**2**	**2**	**2**
Corytophanidae	4	1	4	4
Dactyloidae	14	8	14	9
Diploglossidae	1	—	1	1
Eublepharidae	1	—	1	1
Gekkonidae	2	2	2	1
Iguanidae	2	2	2	2
Mabuyidae	1	1	1	—
Phrynosomatidae	5	3	5	5
Phyllodactylidae	1	—	1	1
Scincidae	2	2	1	1
Sphaerodactylidae	2	1	2	2
Sphenomorphidae	2	1	1	2
Teiidae	5	5	4	2
Xantusiidae	2	—	2	1
Xenosauridae	1	—	1	—
Subtotal	**45**	**26**	**42**	**32**
Boidae	1	1	1	1
Colubridae	20	10	18	8
Dipsadidae	30	11	26	10
Elapidae	2	1	2	—
Leptotyphlopidae	1	1	—	—
Natricidae	3	3	1	1
Sibynophiidae	1	—	1	—
Typhlopidae	2	1	1	—
Viperidae	6	1	4	5
Subtotal	**66**	**29**	**54**	**25**
Cheloniidae	2	2	—	—
Chelydridae	1	1	1	1
Dermatemyidae	1	1	1	1
Dermochelyidae	1	1	—	—
Emydidae	1	1	1	1
Geoemydidae	1	1	—	1
Kinosternidae	3	3	2	3
Staurotypidae	2	2	1	2
Subtotal	**12**	**12**	**6**	**9**
Total	**125**	**69**	**104**	**68**
Sum total	**170**	**88**	**145**	**93**

Table 6. Pair-wise comparison matrix of Coefficient of Biogeographic Resemblance (CBR) data of the herpetofaunal relationships for the three physiographic regions in Tabasco, Mexico. Underlined values = number of species in each region; upper triangular matrix values = species in common between two regions; and lower triangular matrix values = CBR values. The formula for this calculation is: CBR = $2C/N_1 + N_2$ (Duellman, 1990), where C is the number of species common to both regions, N_1 is the number of species in the first region, and N_2 is the number of species in the second region. See Table 4 for an explanation of the abbreviations, and Fig. 12 for the UPGMA dendrogram produced from the CBR data.

	Gulf Coastal Plain	Sierra Norte de Chiapas	Sierras Bajas del Petén
Gulf Coastal Plain	**88**	71	61
Sierra Norte de Chiapas	0.61	**145**	79
Sierras Baja de Petén	0.67	0.66	**93**

The eight single-region species in the SBP (Table 7) are as follows (numbers refer to the distributional categories as designated by Wilson et al. [2017]; an asterisk indicates country endemics):

Triprion petasatus 4
Engystomops pustulosus 6
*Bolitoglossa alberchi**
*Scincella gemmingeri**
Coniophanes schmidti 4
Leptodeira frenata 4
Agkistrodon russeolus 4
Crotalus tzabcan 4

Two of these eight species (25.0%) are country endemics and the remaining six are non-endemics. Of the six non-endemic species, one is an MXSA species and the other five are MXCA species.

In summary, of the 69 single-region species distributed in Tabasco, 51 (73.9%) are non-endemics, 16 (23.2%) are country endemics, and two (2.9%) are non-natives. Of the three physiographic regions in Tabasco, the SNC is of greatest conservation importance, given that it supports the largest overall number of species (145), as well as the largest numbers of single-region species (50) and country-endemics (13).

We constructed a Coefficient of Biogeographic Resemblance (CBR) matrix for establishing the herpetofaunal similarity relationships among the three physiographic regions in Tabasco (Table 6). The SNC supports the highest level of species richness at 145 species, followed by 93 in the SBP, and 88 in the GCP. The mean species richness for the three regions is 108.7. The numbers of shared species among all regional pairs range from 61 between the GCP and the SBP to 79 between the SNC and the SBP. The average value of shared species among all three regions is 70.3.

The CBR data in Table 6 demonstrate values ranging from 0.61 to 0.67 (see below), with a mean value of 0.65. This range of CBR values is limited and the values are relatively high, indicating that many of these species are widespread.

We determined the numbers of species inhabiting one, two, and three of the recognized physiographic regions (Table 7). In each of the two smaller herpetofaunas for the Gulf Coastal Plain and the Sierras Bajas del Petén subregion the numbers of species found in one, two, and three regions increase from the lowest to the highest value. However, in the area with the largest herpetofauna (145 species), the Sierra de Norte de Chiapas, the number of single-region species (50) is higher than the number of the double-region species (40), and is closer to the number of species occupying all three regions (55). Of the 170 total herpetofaunal species in Tabasco, 101 (59.4%) are found in two or three physiographic regions, leaving 69 (40.6%) with a distribution in only a single region (see above). Thus, 50 of these 69 single-region species are restricted to the Sierra Norte de Chiapas.

The highest CBR value (0.67) is that between the GCP and the SBP, and the lowest value (0.61) is between the GCP and the SNC. We expected a relatively high level of resemblance among these three areas, since the two higher-elevation regions are adjacent to the lower-elevation region, and all three regions contain relatively low elevations (see above).

The overall CBR values among the three physiographic regions are as follows, arranged from the highest to lowest value (species numbers in parentheses):

GCP (88) – 0.61 – SNC (145)
SBP (93) – 0.66 – SNC (145)
GCP (88) – 0.67 – SBP (93)

Table 7. Counts of the number of species within each of the three physiographic regions in Tabasco, Mexico, which occupy one, two, or three of the physiographic regions.

Physiographic region	Number of regions inhabited			Total
	One	Two	Three	
Gulf Coastal Plain	11	22	55	88
Sierra del Norte de Chiapas	50	40	55	145
Sierras Baja del Petén	8	30	55	93
State total	**69**	**46**	**55**	**170**

No. 13. *Bolitoglossa veracrucis* Taylor, 1951. The Veracruz Salamander previously was known only from the type locality (Veracruz, Mexico), at 100 to 1,000 m elevation (https://amphibiansoftheworld.amnh.org/). In 2008, however, a population of this species was recorded for the first time in the state of Tabasco, from Cuevas de Muku Chem, in the municipality of Tacotalpa (Gerónimo-Torres et al. 2022). Wilson et al. (2013b) calculated its EVS as 17, placing it in the middle portion of the high vulnerability category. Its conservation status has been considered as Endangered (EN) by IUCN, and as a species of Special Protection (Pr) by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

No. 14. *Corytophanes cristatus* (Merrem, 1820). The Smooth Helmeted Iguana is found at low and intermediate elevations on the Gulf and Caribbean slopes from central Veracruz to Colombia (Lee 1996). This lizard ranges from central Veracruz and the southern part of the Yucatan Peninsula in Mexico, southward on the Atlantic versant and lowlands of Central America through northern Guatemala and Belize to Costa Rica, where it occurs on both the Atlantic and Pacific slopes into northwestern Colombia (Campbell 1998). This individual was found in the municipality of Tacotalpa, Tabasco, in secondary vegetation. Its EVS has been determined as 11, placing it in the middle portion of the medium vulnerability category, and its IUCN status has been assessed as Least Concern (LC). This species was allocated to the Special Protection (Pr) category by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

No. 15. *Corytophanes hernandesii* (Wiegmann, 1831). Hernandez's Helmeted Basilisk occurs at low and moderate elevations on the Atlantic versant from southeastern San Luis Potosí, Mexico, to northwestern Honduras (McCranie et al. 2004). This individual was encountered in the Ejido Villa Guadalupe of Huimanguillo, Tabasco. Wilson et al. (2013a) determined its EVS as 13, placing it at the upper limit of the medium vulnerability category. Its conservation status has not been determined by the IUCN, but this species was provided Special Protection (Pr) status by SEMARNAT. *Photo by José del Carmen Gerónimo-Torres.*

No. 16. *Norops barkeri* Schmidt, 1939. Barker's Anole is a semiaquatic anole endemic to southern Mexico. This species is known from states of Veracruz, Chiapas, Oaxaca, and Tabasco (Powell and Birt 2001). This individual was found in the Ejido Villa Guadalupe of Huimanguillo, Tabasco. This lizard's EVS has been assessed as 15, placing it in the lower portion of the high vulnerability category (Wilson et al. 2013a). Its IUCN status has been determined as Vulnerable (VU), and it is considered a species of Special Protection (Pr) by SEMARNAT. *Photo by Jenny del C.-Estrada-Montiel.*

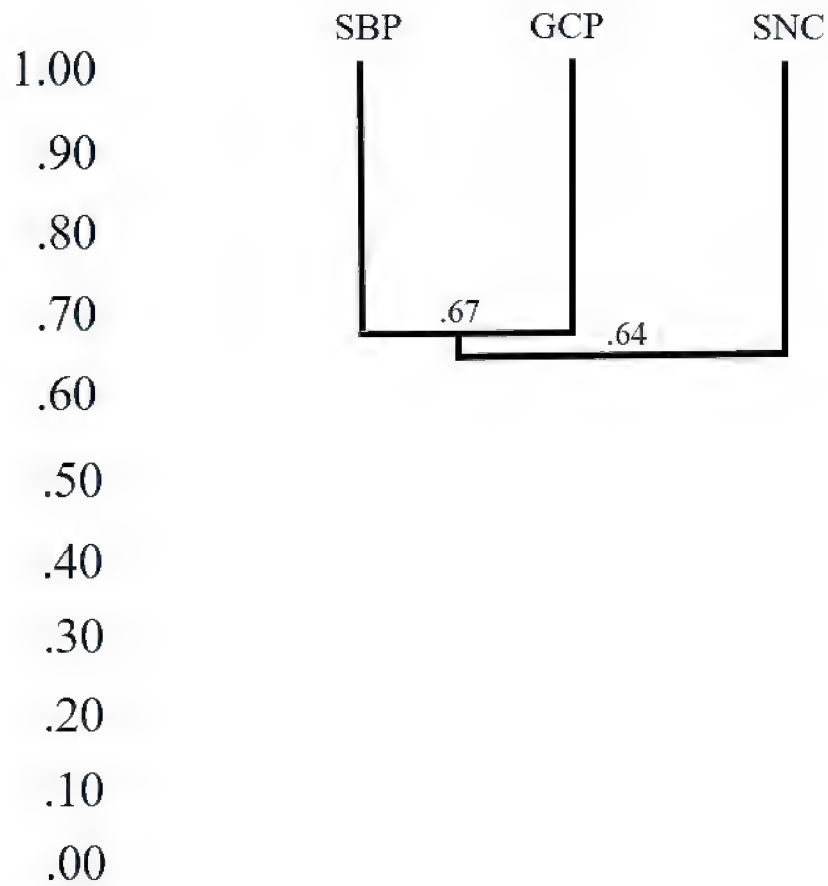

Fig. 5. UPGMA-generated dendrogram illustrating the similarity relationships of species richness among the herpetofaunal components in the three physiographic regions of Tabasco (based on the data in Table 6; Sokal and Michener 1958). Similarity values were calculated using Duellman's (1990) Coefficient of Biogeographic Resemblance (CBR).

Based on the data in Table 6, we created a UPGMA dendrogram (Fig. 5) to demonstrate the herpetofaunal resemblance patterns among the three physiographic regions in Tabasco (see map, Fig. 1). The dendrogram indicates that the CBP and GCP cluster at the 0.67 level and the SNC clusters to the previous pair at the 0.64 level. This overall pattern indicates that all three regions are closely aligned together at an intermediate level of resemblance.

Distribution Status Categorizations

We utilized the same system as Alvarado-Díaz et al. (2013) to examine the distribution status of members of the Tabasco herpetofauna, and this system has been used in all the subsequent entries in the MCS (see above). The categories in this system are non-endemic, country endemic, state endemic (of which none occur in Tabasco), and non-native. These categorizations are listed in Table 8 and summarized in Table 9.

The numbers of species in each of the three applicable categories, in decreasing order of size, are as follows: non-endemics, 145 (85.3% of total of 170 species); country endemics, 20 (11.8%); and non-natives, five (2.9%). As with the states of Oaxaca (Mata-Silva et al. 2015), Chiapas (Johnson et al. 2015a), Tamaulipas (Terán-Juárez et al. 2016), Nuevo León (Nevárez-de los Reyes et al. 2016), Coahuila (Lazcano et al. 2019), and Veracruz (Torres-Hernández et al. 2021), as well as the tri-state Yucatan Peninsula (González-Sánchez et al. 2017), most of the herpetofaunal taxa in Tabasco fall within the non-endemic category. In the other six states evaluated in the Mexican Conservation Series, the largest number falls within the country endemic category: Michoacán (Alvarado-Díaz et al. 2013); Nayarit (Woolrich-Piña et al. 2016); Jalisco (Cruz-Sáenz et al. 2017); Puebla (Woolrich-Piña et al. 2017); Hidalgo (Ramírez-Bautista et al. 2020); and Querétaro (Cruz-Elizalde et al. 2022).

Twenty country endemic species are present in Tabasco, and perhaps this relatively low number was expected because the state lies largely on the Gulf Coastal Plain and adjacent to relatively low-elevation areas, which generally are not known for significant herpetofaunal endemism. No state endemic species occur in Tabasco. In the 13 previous entries in the MCS (including the Oaxaca update; Mata-Silva et al. 2021), the number of state endemic species ranges from one in Nayarit and Nuevo León (Woolrich-Piña et al. 2016; Nevárez-de los Reyes 2016) to 105 in Oaxaca (Mata-Silva et al. 2021).

Five non-native species have been recorded from Tabasco, including *Eleutherodactylus planirostris*, *Norops sagrei*, *Hemidactylus frenatus*, *H. turcicus*, and *Virgotyphlops braminus*. Two of these five species (*H. frenatus* and *V. braminus*) are the most widespread of the non-native species recorded in the 13 entries in the MCS (Cruz-Elizalde et al. 2022), and to date they have been reported in 13 states or tri-state regions.

Wilson et al. (2017) introduced a system for the distributional categorization of the Mesoamerican herpetofauna. The data for the categories applicable to this work are summarized in Table 10. Previously, we noted that 145 species are non-endemic to Tabasco, and we allocated them to six of the nine categories developed by Wilson et al. (2017), including MXUS, MXCA, MXSA, USCA, USSA, and OCEA. As expected, the greatest number and proportion of species fall into the MXCA category (95, or 65.5%), given the proximity of Tabasco to Central America and since a significant portion of its eastern border is shared with Guatemala. Interestingly, the next largest number and proportion of species are allocated to the MXSA category (34, or 23.4%). Oddly, only a single species (0.7%) is assigned to the MXUS category. By way of comparison, this category contains 29 species, or 17.2%, in the herpetofauna of the adjacent state to the west (i.e., Veracruz; Torres-Hernández et al. 2021). The remaining 15 species are in the USCA (eight, or 5.5%), USSA (four, or 2.7%), and OCEA (three, or 2.1%) categories.

Principal Environmental Threats

Deforestation

Deforestation in southeastern Mexico is a serious matter that has worsened over time, and the state of Tabasco is no exception (Fig. 6). The continuous loss of vegetational

No. 17. *Norops compressicauda* Smith and Kerster, 1955. The Malposo Scaly Anole is endemic to Mexico. This anole has been reported from the states of Oaxaca, Veracruz, and Chiapas. Here we present the first records of this species from the state of Tabasco, from the municipalities of Teapa and Tacotalpa, in montane areas at elevations from 100 to 700 m (Ríos Rodas et al. 2017). Wilson et al. (2013a) calculated its EVS as 15, placing it in the lower portion of the high vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN, but this species is not listed by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

No. 18. *Coleonyx elegans* Gray, 1845. The Yucatan Banded Gecko is distributed on the Gulf and Pacific slopes in the states of the southeastern region of Mexico. In Tabasco, this species has been recorded in the municipalities of Tacotalpa, Huimanguillo, and Teapa. This individual is from Muku Chem, in the municipality of Tacotalpa, Tabasco. Its EVS has been determined as 9, placing it at the upper limit of the low vulnerability category (Wilson et al. 2013a). Its IUCN status has been assessed as Least Concern (LC), and as Threatened (A) by SEMARNAT. *Photo by Manuel Hernández-May.*

No. 19. *Ctenosaura similis* (Gray, 1831). The Common Spiny-tailed Iguana occurs at low and moderate elevations from southern Veracruz and Oaxaca southward to Panama (Lee 1996). The native range of this species extends along the Atlantic versant from the Isthmus of Tehuantepec southeastward to northeastern Nicaragua, and on the Pacific versant from the Isthmus of Tehuantepec southeastward to Panama (Köhler 2003). This individual was found in rainforest at an elevation of 200 m, in the municipality of Tenosique, Tabasco. Wilson et al. (2013a) calculated its EVS as 8, placing it in the upper portion of the low vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN. This species was allocated to the Threatened (A) category by SEMARNAT. *Photo by María del Rosario Barragán-Vázquez.*

No. 20. *Sceloporus teapensis* Günther, 1890. The Teapen Rosebellied Lizard occurs at low elevations on the Atlantic slopes from southern Veracruz and Oaxaca, eastward through Chiapas, Tabasco, and Campeche, and through the Petén region of Guatemala to Belize, and south to Cobán, Alta Verapaz, Guatemala (Lee 1996). This individual was encountered in the Ejido Villa Guadalupe of Huimanguillo, Tabasco. Wilson et al. (2013a) determined its EVS as 13, placing it at the upper limit of the medium vulnerability category. Its conservation status has been assessed as Least Concern (LC) by the IUCN, but has not been determined by SEMARNAT. *Photo by Jenny del Carmen Estrada-Montiel.*

Fig. 6. Deforestation due to road construction in the vicinity of Paraíso, Tabasco. *Photo by José del Carmen Gerónimo-Torres.*

Fig. 7. Conversion of land use for agricultural purposes in the community of Villa Luz, in the municipality of Tacotalpa, Tabasco. *Photo by Liliana Ríos-Rodas.*

cover in tropical forest has been precipitated primarily by a shift in land use for livestock and agricultural activities, lumber extraction, an increasing number of roads, oil production-related activities, and the direct effect of human population growth (Maldonado-Sánchez et al. 2016). To date, Tabasco has lost more than 90% of its original vegetational cover (Zavala-Cruz and Castillo 2003), and more recent data indicate that approximately only 2% of this vegetation remains (Sánchez-Munguía 2005). In the basins of the Grijalva and Usumacinta rivers, the tropical forest cover has been reduced from 36% in 1993 to only 9% in 2007 (Kolb and Galicia 2012).

The above numbers reveal the somber panorama that Tabasco currently faces, which directly affects the prospects for conserving biodiversity, including its herpetofauna. The last remnants of forest in Tabasco are distributed mostly in the municipalities of Teapa, Tenosique, Huimanguillo, and Macuspana (Castillo and Zavala 1996); ironically, these are the same geographic entities where various extension records of amphibians and reptiles have been reported in recent years. Species such as the Northern Glass Frog (*Hyalinobatrachium viridissimum*), the Chiapan Highlands Treefrog (*Exerodonta bivocata*), the Smooth-headed Helmeted Basilisk, locally known as Turipache (*Corytophanes cristatus*), Barker's Anole (*Norops barkeri*), and the Keeled Earth Snake (*Geophis carinosus*) are just a few worthy of mention. These records highlight the need for continuous and urgent exploration, especially in areas that still contain tropical forest.

Agricultural Activities

As mentioned earlier, one of the main drivers of deforestation is farming (Fig. 7) and livestock activities. In this regard, Alejandro-Montiel et al. (2010) stated that these activities are responsible for 94% of the land change that has taken place in Tabasco. Noteworthy agricultural policies for Tabasco were developed in the 1960s and 1970s (Plan Chontalpa and Plan Balancán-Tenosique), and have affected more than 200,000 ha, resulting in the complete elimination of evergreen tropical forest and the desiccation of wetlands for the later development of urban communities (Barkin 1978). For example, immediately after the completion of one of these projects, a subsequent study revealed that only 8% of the forests remained in the municipalities of Balancán and Tenosique, which increased flooding and soil erosion in those areas (Tudela 1989; Torres-Masuera 2021).

These programs did not have the promised results, but on the contrary were responsible for the loss of forest and biodiversity that have not recovered thus far. This infamous action was never reported; therefore, there are no actual numbers that can reveal the specific amount of biodiversity affected.

Currently, Tabasco dedicates more than 253,000 ha to the cultivation of banana, sugarcane, cocoa, corn, and oil palm. Unfortunately, these large-scale crops are damaging to the remaining natural ecosystems in the state, whose effects are exacerbated by the large amount of associated chemicals. The municipalities of Huimanguillo and Balancán have the largest amount of land used for cultivation, and Huimanguillo also has the largest livestock production (Infografía Agroalimentaria 2017). At the same time, the municipality of Huimanguillo contains remnants of evergreen tropical forest where additional species have been reported in recent times, expanding their geographic distributions. The current and historical situation regarding the development of agriculture in the state also indicates the continuous damage inflicted on natural ecosystems and, therefore, all of the species they harbor.

Roads

Roads represent an important contributor to the intensification of productivity in communities, and simultaneously are an instrumental component for social, economic, and cultural integration. According to INEGI (2009), Tabasco has an extensive system of roads, and is

No. 21. *Sphaerodactylus continentalis* Werner, 1896. The Upper Central American Geckolet occurs at "low and moderate elevations from the Isthmus of Tehuantepec in northern Oaxaca, Mexico, to about the Catacamas, Olancho, region of east-central Honduras;" this species "also occurs on Utila Island in the Honduran Bay Islands and possibly on Cozumel Island, Quintana Roo, Mexico" (McCranie and Hedges 2012). This individual is from Muku Chem, in the municipality of Tacotalpa, Tabasco. Mata-Silva et al. (2021) determined its EVS as 10, placing it at the lower limit of the medium vulnerability category. Its conservation status has been evaluated as Least Concern (LC) by the IUCN, but it has not been assessed by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

No. 22. *Holcosus stuarti* Smith, 1940. The Rainbow Ameiva occurs on the "Atlantic slopes of Mexico from the middle of the Isthmus of Tehuantepec eastward in the lowlands to the southern borders of Laguna de Términos and to Tenosique, Tabasco; southward up the valley of the Río Grijalva at least as far as Tuxtla Gutiérrez, Chiapas" (Meza-Lázaro and Nieto-Montes de Oca 2015). This individual was located in the Ejido Villa Guadalupe of Huimanguillo, Tabasco. Wilson et al. (2013a) determined its EVS as 7, placing it in the middle limit of the low vulnerability category. Its conservation status has been evaluated as Least Concern (LC) by the IUCN, but this species is not listed by SEMARNAT. *Photo by Jenny del Carmen Estrada-Montiel.*

No. 23. *Lepidophyma flavimaculatum* Duméril, 1851. The Yellow-spotted Night Lizard is found at low and moderate elevations on the Atlantic slope from Veracruz eastward through northern Guatemala, Belize, and northern Honduras. In the Yucatan Peninsula it is known from northeastern Chiapas, El Petén, Belize, and southern Quintana Roo (Lee 1996). This individual was located in the Ejido Villa Guadalupe of Huimanguillo, Tabasco. Wilson et al. (2013a) assessed its EVS as 8, placing it in the upper portion of the low vulnerability category. Its conservation status has been evaluated as Least Concern (LC) by the IUCN, and this species was placed in the Special Protection (Pr) category by SEMARNAT. *Photo by José del Carmen Gerónimo-Torres.*

No. 24. *Leptophis mexicanus* Duméril, Bibron, and Duméril, 1854. The Mexican Parrot Snake is distributed in southeastern Mexico, including Chiapas, Veracruz, Oaxaca, Tabasco, Yucatán, Campeche, San Luis Potosí, Querétaro, Tamaulipas, Puebla, Hidalgo, Nuevo León, Guerrero, and Yucatan Peninsula, into Guatemala, Honduras, Belize, El Salvador, Nicaragua, and Costa Rica. In Guatemala it occurs from near sea level to about 1,360 m in elevation (Lee 1996; Campbell 1998). This individual was found in the municipality of Tacotalpa, Tabasco, in secondary vegetation (*acahual*). Its EVS has been determined as 6, placing it in the middle portion of the low vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN and it is allocated to the Threatened (A) category by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

Fig. 8. Roads. A *Boa imperator* dead on the road in the Pantanos de Centla Biosphere Reserve, in the municipality of the same name, Tabasco. *Photo by Coral J. Pacheco-Figueroa.*

Fig. 9. Deforestation due to oil activities in the vicinity of Paraíso, Tabasco. *Photo by José del Carmen Gerónimo-Torres.*

among the three best-served states in the country, with an index of 248 m/km² (Vidal-García and Negrete 2019). The construction and functioning of roads are elements that have drastic and long-term consequences on the natural landscape, as they significantly affect the survival of the native herpetofauna (Trombulak and Frissell 2000; Coffin 2007). The building and maintenance of roads implies the unavoidable removal of native vegetation cover, thus enabling a series of linked processes that ultimately lead to the detriment of adjacent habitats. With respect to the mortality of fauna on roads (Fig. 8), Pozo-Montuy et al. (2019) reported 111 individuals killed by vehicles on the road from Villahermosa to Zacatal; of those, 22.5% were reptiles and 20.7% amphibians. The species affected more frequently were in the families Iguanidae, Boidae, Colubridae, Viperidae, and Geoemydidae; more specifically for lizards they included Green Iguanas (*Iguana rhinolopha*) and Black Iguanas (*Ctenosaura similis*) (Canales-Delgadillo et al. 2020). Other studies carried out in the state reported the killing of *I. rhinolopha* on highway 186 (Villahermosa-Aeropuerto) and the Cane Toad (*Rhinella horribilis*) on the Tabascan plains. Lastly, a survey conducted at Reserva de la Biósfera Pantanos de Centla showed that 43% of the road-kills were amphibians, primarily Brown's Leopard Frog (*Lithobates brownorum*) (Pacheco-Figueroa 2021).

Soil Pollution and Oil-related Activities

In Tabasco, the municipalities with the highest numbers of oil spills that affected numerous hectares of land from 1995 until 2001 were Cardenas, Huimanguillo, Cunduacan, and Comalcalco (Ochoa-Gaona et al. 2011). The long history of oil spills and gas explosions in Tabasco (Fig. 9) has led to serious consequences in many communities, because this activity also resulted in the pollution of soils and vegetation such as grasslands (Zavala-Cruz et al. 2005). Some studies have identified approximately 7,500 ha that are affected, more than 90% of which are located in wetlands (Adams-Schroeder 1999; Beltrán-Paz 2006). It was estimated that 0.07% of the state was polluted with fossil fuels (Rivera-Cruz and Trujillo-Narcía 2004; Ferrera-Cerrato et al. 2006). All amphibian groups found in Tabasco have been affected by the oil industry, although a study by Reynoso-Rosales (1999) in southeastern Mexico, including Tabasco, determined that the detriment to amphibians is the result of a combined effect from both farming and the oil industry. With respect to the latter activity, this includes consecutive processes such as exploration, perforation, and production. Among the direct effects from the oil industry are the disturbances caused by permanent light sources at all installations, which likely affect the behavior of species present around these industrial facilities. For instance, toads (*Rhinella* and *Incilius*) congregate at light sources to search for food.

Myths and Cultural Factors

With respect to the herpetofauna, ethnozoological knowledge includes symbolic, spiritual, and social meanings in indigenous societies (Ávila-Nájera et al. 2018), although few studies have addressed this subject in Tabasco. Among the most frequent uses of native herpetofauna are for food (iguanas, turtles, and crocodiles, Hernández-López et al. 2012) and magic-religious uses in conjunction with medicinal application. For example, rattlesnakes (*Crotalus*) are used to treat cancer, diabetes, acne, and skin health issues (Gómez-Álvarez and Pacheco 2010). On the other hand, snakes generally are considered as dangerous, and their encounters usually result in their immediate elimination. A similar situation is experienced by amphibians, which are considered mostly as undesirable.

People in Tabasco have consumed native terrestrial vertebrates for millennia, primarily reptiles, birds, and mammals as food, as well as for skins, pets, and medicinal purposes (Pozo-Montuy et al. 2019). To date, 16 species of reptiles have been identified as traditionally consumed in Tabasco, such as iguanas, turtles, snakes,

No. 25. *Oxybelis potosiensis* (Taylor, 1941). The Gulf Coast Vine Snake is distributed from San Luis Potosí and northern Veracruz, southward to Yucatán, Mexico, and Belize (Jadin et al. 2020). This individual was found in the municipality of Huimanguillo, Tabasco. Its EVS has been determined as 5 (Cruz-Elizalde et al. 2022), placing it in the lower portion of the low vulnerability category. Its conservation status has not been evaluated (NE) by the IUCN, and it is considered as having No Status (NS) by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

No. 26. *Coniophanes imperialis* (Baird and Girard, 1859). The Black-striped Snake occurs at low and moderate elevations on the Atlantic slope from southern Texas southward on the Atlantic watershed through eastern Mexico, Yucatán, Belize, and northern and eastern Guatemala to Honduras; it also occurs locally on Pacific slopes in Oaxaca, Chiapas, Yucatán, Campeche, and Quintana Roo (Lee 1996; Campbell 1998). This individual was found in the municipality of Huimanguillo, Tabasco. Its EVS has been determined as 8, placing it in the upper portion of the low vulnerability category. Its conservation status has been established as Least Concern (LC) by the IUCN, but has been assigned No Status (NS) by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

No. 27. *Enulius flavitorques* (Cope, 1868). The Pacific Long-tailed Snake occurs at low and moderate elevations on the Pacific versant from Jalisco, Mexico, to Panama, and on the Atlantic versant in Chiapas, Mexico, Honduras (including Isla Utila in the Islas de la Bahía), Panama, northern Colombia, and northwestern Venezuela (Hernández-Valadez et al. 2016). This individual was found in a coconut plantation in Playa Chiltepec, in the municipality of Paraiso, Tabasco. Its EVS has been determined as 5, placing it in the lower portion of the low vulnerability category. Its conservation status has been evaluated as Least Concern (LC) by the IUCN, but its status remains undetermined (NS) by SEMARNAT. *Photo by Marco Antonio López-Luna.*

No. 28. *Imantodes cenchoa* (Linnaeus, 1758). The Neotropical Blunt-headed Treesnake occurs at low and moderate elevations in Mexico, from Chiapas on the Pacific slope and Tamaulipas on the Atlantic slope, southward throughout most of the Petén region in Guatemala and the northeastern portion of Yucatan Peninsula, through the remainder of Central America to Argentina and Paraguay (Lee 1996; Campbell 1998). This individual was found in Muku Chem, in the municipality of Tacotalpa, Tabasco. Wilson et al. (2013a) determined its EVS as 6, placing it in the middle portion of the low vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN, and as a species of Special Protection (Pr) by SEMARNAT. *Photo by José del Carmen Gerónimo-Torres.*

Table 8. Distributional and conservation status measures for members of the herpetofauna of Tabasco, Mexico. Distributional status: CE = endemic to country of Mexico; NE = not endemic to state or country; and NN = non-native. The numbers suffixed to the "NE" category signify the distributional categories developed by Wilson et al. (2017) and implemented in the taxonomic list at the *Mesoamerican Herpetology* website (http://mesoamericanherpetology.com), as follows: 3 (species distributed only in Mexico and the USA); 6 (species ranging from Mexico to South America); 7 (species ranging from the USA to Central America); and 8 (species ranging from the USA to South America). Environmental Vulnerability Score (taken from Wilson et al. 2013a,b): low (L) vulnerability species (EVS of 3–9); medium (M) vulnerability species (EVS of 10–13); and high (H) vulnerability species (EVS of 14–20). IUCN Categorization: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient; NE = Not Evaluated. SEMARNAT Status: A = Threatened; P = Endangered; Pr = Special Protection; and NS = No Status. See Alvarado-Díaz et al. (2013), Johnson et al. (2015a), and Mata-Silva et al. (2015) for explanations of the EVS, IUCN, and SEMARNAT rating systems.

Taxa	Distributional status	Environmental Vulnerability Category (score)	IUCN categorization	SEMARNAT status
Incilius macrocristatus	NE4	M (11)	VU	NS
Incilius valliceps	NE4	L (6)	LC	NS
Rhinella horribilis	NE7	L (3)	NE	NS
Hyalinobatrachium viridissimum	NE4	M (10)	LC	NS
Craugastor alfredi	NE4	M (11)	VU	NS
*Craugastor berkenbuschii**	CE	H (14)	NT	Pr
Craugastor laticeps	NE4	M (12)	NT	Pr
Craugastor loki	NE4	M (10)	LC	NS
Craugastor palenque	NE4	H (15)	DD	NS
*Craugastor pelorus**	CE	H (15)	DD	NS
*Craugastor rhodopis**	CE	H (14)	VU	NS
Eleutherodactylus leprus	NE4	M (12)	VU	NS
*Eleutherodactylus planirostris***	NN	—	—	—
*Charadrahyla chaneque**	CE	M (13)	EN	Pr
Dendropsophus ebraccatus	NE6	M (10)	LC	NS
Dendropsophus microcephalus	NE6	L (7)	LC	NS
*Duellmanohyla chamulae**	CE	M (13)	EN	Pr
*Exerodonta bivocata**	CE	H (15)	DD	NS
Ptychohyla macrotympanum	NE4	M (11)	CR	NS
*Quilticohyla zoque**	CE	H (14)	NE	NS
*Rheohyla miotympanum**	CE	L (9)	NT	NS
Scinax staufferi	NE4	L (4)	LC	NS
Smilisca baudinii	NE7	L (3)	LC	NS
Smilisca cyanosticta	NE4	M (12)	NT	NS
Tlalocohyla loquax	NE4	L (7)	LC	NS
Tlalocohyla picta	NE4	L (8)	LC	NS
Trachycephalus vermiculatus	NE6	L (4)	LC	NS
Triprion petasatus	NE4	M (10)	LC	Pr
Triprion spinosus	NE4	H (14)	LC	NS
Engystomops pustulosus	NE6	L (7)	LC	NS
Leptodactylus fragilis	NE8	L (5)	LC	NS
Leptodactylus melanonotus	NE6	L (6)	LC	NS
Gastrophyrne elegans	NE4	L (8)	LC	Pr
Hypopachus variolosus	NE7	L (4)	LC	NS
Agalychnis moreletii	NE4	L (7)	CR	NS
Agalychnis taylori	NE4	M (11)	LC	NS
Lithobates brownorum	NE4	L (8)	NE	Pr
Lithobates vaillanti	NE6	L (9)	LC	NS
Rhinophrynus dorsalis	NE7	L (8)	LC	NS
*Bolitoglossa alberchi**	CE	H (15)	VU	NS
Bolitoglossa mexicana	NE4	M (11)	LC	Pr
*Bolitoglossa platydactyla**	CE	H (15)	NT	Pr
Bolitoglossa rufescens	NE4	L (9)	LC	Pr

Table 8 (continued). Distributional and conservation status measures for members of the herpetofauna of Tabasco, Mexico. Distributional status: CE = endemic to country of Mexico; NE = not endemic to state or country; and NN = non-native. The numbers suffixed to the "NE" category signify the distributional categories developed by Wilson et al. (2017) and implemented in the taxonomic list at the *Mesoamerican Herpetology* website (http://mesoamericanherpetology.com), as follows: 3 (species distributed only in Mexico and the USA); 6 (species ranging from Mexico to South America); 7 (species ranging from the USA to Central America); and 8 (species ranging from the USA to South America). Environmental Vulnerability Score (taken from Wilson et al. 2013a,b): low (L) vulnerability species (EVS of 3–9); medium (M) vulnerability species (EVS of 10–13); and high (H) vulnerability species (EVS of 14–20). IUCN Categorization: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient; NE = Not Evaluated. SEMARNAT Status: A = Threatened; P = Endangered; Pr = Special Protection; and NS = No Status. See Alvarado-Díaz et al. (2013), Johnson et al. (2015a), and Mata-Silva et al. (2015) for explanations of the EVS, IUCN, and SEMARNAT rating systems.

Taxa	Distributional status	Environmental Vulnerability Category (score)	IUCN categorization	SEMARNAT status
*Bolitoglossa veracrucis**	CE	H (17)	EN	Pr
Dermophis mexicanus	NE4	M (11)	VU	Pr
Crocodylus acutus	NE8	H (14)	VU	Pr
Crocodylus moreletii	NE4	M (13)	LC	Pr
Basiliscus vittatus	NE4	L (7)	LC	NS
Corytophanes cristatus	NE6	M (11)	LC	Pr
Corytophanes hernandezii	NE4	M (13)	LC	Pr
Laemanctus longipes	NE4	L (9)	LC	Pr
*Norops barkeri**	CE	H (15)	VU	Pr
Norops beckeri	NE4	M (12)	NE	Pr
Norops biporcatus	NE6	M (10)	NE	Pr
Norops capito	NE4	N (13)	NE	NS
*Norops compressicauda**	CE	H (15)	LC	NS
Norops laeviventris	NE4	L (9)	NE	NS
Norops lemurinus	NE4	L (8)	NE	NS
Norops petersi	NE4	L (9)	NE	NS
Norops rodriguezii	NE4	M (10)	NE	NS
*Norops sagrei***	NN	—	—	—
Norops sericeus	NE4	L (8)	NE	NS
Norops tropidonotus	NE4	L (9)	NE	NS
Norops uniformis	NE4	M (13)	NE	NS
Norops unilobatus	NE4	L (7)	NE	NS
Celestus rozellae	NE4	M (13)	NT	Pr
Coleonyx elegans	NE4	L (9)	LC	A
*Hemidactylus frenatus***	NN	—	—	—
*Hemidactylus turcicus***	NN	—	—	—
Ctenosaura similis	NE4	L (8)	LC	A
Iguana rhinolopha	NE6	M (10)	NE	Pr
Marisora lineola	NE4	M (10)	NE	NS
Sceloporus chrysostictus	NE4	M (13)	LC	NS
Sceloporus lundelli	NE4	H (14)	LC	NS
Sceloporus serrifer	NE4	L (6)	LC	NS
Sceloporus teapensis	NE4	M (13)	LC	NS
Sceloporus variabilis	NE4	L (5)	NE	NS
Thecadactylus rapicauda	NE6	M (10)	NE	Pr
Mesoscincus schwartzei	NE4	M (11)	LC	NS
Plestiodon sumichrasti	NE4	M (12)	LC	NS
Sphaerodactylus continentalis	NE4	M (10)	NE	NS
Sphaerodactylus glaucus	NE4	M (12)	LC	Pr
Scincella cherriei	NE4	L (7)	NE	NS
*Scincella gemmingeri**	CE	M (11)	LC	Pr
Aspidoscelis deppii	NE4	L (8)	LC	NS
*Aspidoscelis guttatus**	CE	M (12)	LC	NS
*Holcosus amphigrammus**	CE	M (11)	NE	NS

Table 8 (continued). Distributional and conservation status measures for members of the herpetofauna of Tabasco, Mexico. Distributional status: CE = endemic to country of Mexico; NE = not endemic to state or country; and NN = non-native. The numbers suffixed to the "NE" category signify the distributional categories developed by Wilson et al. (2017) and implemented in the taxonomic list at the *Mesoamerican Herpetology* website (http://mesoamericanherpetology.com), as follows: 3 (species distributed only in Mexico and the USA); 6 (species ranging from Mexico to South America); 7 (species ranging from the USA to Central America); and 8 (species ranging from the USA to South America). Environmental Vulnerability Score (taken from Wilson et al. 2013a,b): low (L) vulnerability species (EVS of 3–9); medium (M) vulnerability species (EVS of 10–13); and high (H) vulnerability species (EVS of 14–20). IUCN Categorization: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient; NE = Not Evaluated. SEMARNAT Status: A = Threatened; P = Endangered; Pr = Special Protection; and NS = No Status. See Alvarado-Díaz et al. (2013), Johnson et al. (2015a), and Mata-Silva et al. (2015) for explanations of the EVS, IUCN, and SEMARNAT rating systems.

Taxa	Distributional status	Environmental Vulnerability Category (score)	IUCN categorization	SEMARNAT status
Holcosus festivus	NE6	M (11)	LC	NS
*Holcosus stuarti**	CE	M (12)	NE	NS
Lepidophyma flavimaculatum	NE4	L (8)	LC	Pr
*Lepidophyma tuxtlae**	CE	M (11)	DD	A
Xenosaurus rackhami	NE4	M (11)	NE	NS
Boa imperator	NE6	M (10)	NE	NS
Dendrophidion vinitor	NE4	M (13)	LC	NS
Drymarchon melanurus	NE6	L (6)	LC	NS
Drymobius margaritiferus	NE8	L (6)	NE	NS
Ficimia publia	NE4	L (9)	LC	NS
Lampropeltis polyzona	NE6	L (9)	NE	NS
Leptophis ahaetulla	NE6	M (10)	NE	A
Leptophis mexicanus	NE4	L (6)	LC	A
Masticophis mentovarius	NE6	L (6)	LC	A
Mastigodryas melanolomus	NE4	L (6)	LC	NS
Oxybelis fulgidus	NE6	L (9)	NE	NS
Oxybelis potosiensis	NE4	H (15)	NE	NS
Phrynonax poecilonotus	NE6	M (10)	LC	NS
Pseudelaphe flavirufa	NE4	M (10)	LC	NS
Senticolis triaspis	NE7	L (6)	LC	NS
Spilotes pullatus	NE6	L (6)	NE	NS
Stenorrhina degenhardtii	NE6	L (9)	NE	NS
Stenorrhina freminvillii	NE4	L (7)	NE	NS
Tantilla rubra	NE4	L (5)	LC	Pr
Tantilla schistosa	NE4	L (8)	LC	NS
Tantillita lintoni	NE4	M (12)	LC	Pr
Adelphicos quadrivirgatum	NE4	M (10)	LC	Pr
Amastridium sapperi	NE4	M (10)	LC	NS
Clelia scytalina	NE4	M (13)	LC	NS
Coniophanes bipunctatus	NE4	L (9)	LC	NS
Coniophanes fissidens	NE6	L (7)	NE	NS
Coniophanes imperialis	NE7	L (8)	LC	NS
Coniophanes piceivittis	NE4	L (7)	LC	NS
Coniophanes quinquevittatus	NE4	M (13)	LC	NS
Coniophanes schmidti	NE4	M (13)	LC	NS
Conophis lineatus	NE4	L (9)	LC	NS
Dipsas brevifacies	NE4	H (15)	LC	Pr
Enulius flavitorques	NE6	L (5)	NE	NS
Geophis carinosus	NE4	L (8)	LC	NS
*Geophis laticinctus**	CE	M (11)	LC	Pr
Geophis sanniolus	NE4	M (12)	LC	NS
Geophis sartorii	NE4	L (9)	LC	Pr
Imantodes cenchoa	NE6	L (6)	NE	Pr
Imantodes gemmistratus	NE6	L (6)	NE	Pr

Table 8 (continued). Distributional and conservation status measures for members of the herpetofauna of Tabasco, Mexico. Distributional status: CE = endemic to country of Mexico; NE = not endemic to state or country; and NN = non-native. The numbers suffixed to the "NE" category signify the distributional categories developed by Wilson et al. (2017) and implemented in the taxonomic list at the *Mesoamerican Herpetology* website (http://mesoamericanherpetology.com), as follows: 3 (species distributed only in Mexico and the USA); 6 (species ranging from Mexico to South America); 7 (species ranging from the USA to Central America); and 8 (species ranging from the USA to South America). Environmental Vulnerability Score (taken from Wilson et al. 2013a,b): low (L) vulnerability species (EVS of 3–9); medium (M) vulnerability species (EVS of 10–13); and high (H) vulnerability species (EVS of 14–20). IUCN Categorization: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient; NE = Not Evaluated. SEMARNAT Status: A = Threatened; P = Endangered; Pr = Special Protection; and NS = No Status. See Alvarado-Díaz et al. (2013), Johnson et al. (2015a), and Mata-Silva et al. (2015) for explanations of the EVS, IUCN, and SEMARNAT rating systems.

Taxa	Distributional status	Environmental Vulnerability Category (score)	IUCN categorization	SEMARNAT status
Leptodeira frenata	NE4	M (12)	LC	NS
Leptodeira maculata	NE4	L (7)	LC	Pr
Leptodeira septentrionalis	NE8	L (8)	NE	NS
Ninia diademata	NE4	L (9)	LC	NS
Ninia sebae	NE4	L (4)	LC	NS
Oxyrhopus petolarius	NE6	H (14)	NE	NS
Pliocercus elapoides	NE4	M (10)	LC	NS
Rhadinaea decorata	NE6	L (9)	NE	NS
Sibon dimidiatus	NE4	L (10)	LC	NS
Sibon nebulatus	NE6	L (5)	NE	NS
Tretanorhinus nigroluteus	NE4	M (10)	LC	NS
Xenodon rabdocephalus	NE6	M (13)	NE	NS
*Micrurus diastema**	CE	H (17)	LC	Pr
Micrurus elegans	NE4	M (13)	LC	Pr
Epictia phenops	NE4	L (4)	NE	NS
Nerodia rhombifer	NE3	M (10)	LC	NS
Thamnophis marcianus	NE7	M (10)	LC	A
Thamnophis proximus	NE7	L (7)	LC	A
Scaphiodontophis annulatus	NE4	M (11)	LC	NS
Amerotyphlops tenuis	NE4	M (11)	LC	NS
Virgotyphlops braminus	NN	—	—	—
Agkistrodon russeolus	NE4	H (15)	NE	NS
Bothriechis schlegelii	NE6	M (13)	NE	NS
Bothrops asper	NE6	M (12)	NE	NS
Crotalus tzabcan	NE4	H (16)	LC	NS
Metlapilcoatlus mexicanus	NE4	M (12)	LC	NS
Porthidium nasutum	NE6	H (14)	LC	Pr
Chelonia mydas	NE9	—	EN	P
Lepidochelys kempii	NE9	—	CR	P
Chelydra rossignonii	NE4	H (17)	VU	NS
Dermatemys mawii	NE4	H (17)	CR	P
Dermochelys coriacea	NE9	—	VU	P
Trachemys venusta	NE6	H (19)	VU	NS
Rhinoclemmys areolata	NE4	M (13)	NT	A
Kinosternon acutum	NE4	H (14)	NT	Pr
Kinosternon leucostomum	NE6	M (10)	NE	Pr
Kinosternon scorpioides	NE6	M (10)	NE	Pr
Claudius angustatus	NE4	H (14)	NT	Pr
Staurotypus triporcatus	NE4	H (14)	NT	A

No. 29. *Ninia sebae* (Duméril, Bibron, and Duméril, 1854). The Redback Coffee Snake occurs at low and moderate elevations on the Atlantic slope from Veracruz and the Pacific slope from Oaxaca, Mexico, southeastward and eastward through Central America to Costa Rica (Lee 1996). In Panama it has been recorded in Changuinola district (Ponce et al. 2008). In Guatemala it ranges from near sea level to about 2,000 m in elevation (Campbell 1998). This individual was found in a cornfield in the municipality of Tenosique, Tabasco. Its EVS has been determined as 5 (Wilson et al. 2013a), placing it in the lower portion of the low vulnerability category. Its conservation status has been assessed as Least Concern (LC) by the IUCN, but as Not Evaluated (NS) by SEMARNAT. *Photo by María del Rosario Barragán-Vázquez.*

No. 30. *Sibon dimidiatus* (Günther, 1872). The Slender Snail Sucker occurs at low, moderate, and intermediate elevations on the Pacific slope of Guatemala, and in premontane areas from northern Veracruz, Mexico, southward through Central America to northern Brazil, Colombia, Peru, Venezuela, Guyana, and Ecuador west of the Andes (Lee 1996; Espinal et al. 2021). This individual is from Muku Chem, in the municipality of Tacotalpa, Tabasco. Wilson et al. (2013a) determined its EVS as 10, placing it at the lower limit of the medium vulnerability category. Its conservation status has been assessed as Least Concern by the IUCN, but it has not been assessed by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

No. 31. *Micrurus elegans* Jan, 1858. The Elegant Coral Snake is distributed from Mexico to southwestern Guatemala. In Mexico it has been reported from the states of Chiapas, Oaxaca, Puebla, Veracruz, and in the municipality of Teapa, Tabasco (Soto-Huerta and Clause 2017). This species ranges from 100 to 1,700 m in elevation. This individual was found in the municipality of Tacotalpa, Tabasco. Its EVS has been determined as 13 (Torres-Hernández et al. 2021), placing it at the upper limit of the medium vulnerability category. Its conservation status has been considered as Least Concern (LC) by the IUCN, but it is considered a species of Special Protection (Pr) by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

No. 32. *Epictia phenops* (Cope, 1875). The distribution of the Slender Threadsnake extends "from southern Mexico to western Honduras" (Wallach 2016: 254). This individual was found in the city of Villahermosa. The EVS of this blindsnake has been calculated as 4 (Mata-Silva et al. 2021), placing it in the lower portion of the low vulnerability category. The conservation status of this species has not been assessed by either the IUCN or SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

Table 9. Summary of the distributional status data for herpetofaunal families in Tabasco, Mexico.

Family	Number of species	Distributional status		
		Non-endemic (NE)	Country Endemic (CE)	Non-native (NN)
Bufonidae	3	3	—	—
Centrolenidae	1	1	—	—
Craugastoridae	7	4	3	—
Eleutherodactylidae	2	1	—	1
Hylidae	16	11	5	—
Leptodactylidae	3	3	—	—
Microhylidae	2	2	—	—
Phyllomedusidae	2	2	—	—
Ranidae	2	2	—	—
Rhinophrynidae	1	1	—	—
Subtotal	**39**	**30**	**8**	**1**
Plethodontidae	5	2	3	—
Subtotal	**5**	**2**	**3**	**—**
Dermophiidae	1	1	—	—
Subtotal	**1**	**1**	**—**	**—**
Total	**45**	**33**	**11**	**1**
Crocodylidae	2	2	—	—
Subtotal	**2**	**2**	**—**	**—**
Corytophanidae	4	4	—	—
Dactyloidae	14	11	2	1
Diploglossidae	1	1	—	—
Eublepharidae	1	1	—	—
Gekkonidae	2	—	—	2
Iguanidae	2	2	—	—
Mabuyidae	1	1	—	—
Phrynosomatidae	5	5	—	—
Phyllodactylidae	1	1	—	—
Scincidae	2	2	—	—
Sphaerodactylidae	2	2	—	—
Sphenomorphidae	2	1	1	—
Teiidae	5	2	3	—
Xantusiidae	2	1	1	—
Xenosauridae	1	1	—	—
Subtotal	**45**	**35**	**7**	**3**
Boidae	1	1	—	—
Colubridae	20	20	—	—
Dipsadidae	30	29	1	—
Elapidae	2	1	1	—
Leptotyphlopidae	1	1	—	—
Natricidae	3	3	—	—
Sibynophiidae	1	1	—	—
Typhlopidae	2	1	—	1
Viperidae	6	6	—	—
Subtotal	**66**	**63**	**2**	**1**
Cheloniidae	2	2	—	—
Chelydridae	1	1	—	—
Dermatemyidae	1	1	—	—
Dermochelyidae	1	1	—	—
Emydidae	1	1	—	—
Geoemydidae	1	1	—	—
Kinosternidae	3	3	—	—
Staurotypidae	2	2	—	—
Subtotal	**12**	**12**	**—**	**—**
Total	**125**	**112**	**9**	**4**
Sum Total	**170**	**145**	**20**	**5**

No. 33. *Thamnophis marcianus* (Baird and Girard, 1853). The Checkered Garter Snake occurs at low and moderate elevations throughout the southwestern United States and northern Mexico, and on the Pacific slope of the Isthmus of Tehuantepec. On the Atlantic slope, it ranges from northern Chiapas and eastern Tabasco through the Yucatan Peninsula and southward to Costa Rica (Lee 1996). This individual was found in the municipality of Huimanguillo, Tabasco. Its EVS has been determined as 10 (Wilson et al. 2013a), placing it at the lower limit of the medium vulnerability category. Its conservation status has been assessed as Least Concern (LC) by the IUCN, and it has been allocated to the Threatened (A) category by SEMARNAT. *Photo by Marco Antonio Torrez-Pérez.*

No. 34. *Agkistrodon russeolus* Gloyd, 1972. The distribution of the Mexican Moccasin primarily extends along the outer part of the Yucatan Peninsula, from west-central Campeche and the northern portion of Yucatán and Quintana Roo on the Gulf side, and in northern Belize on the Caribbean side, although isolated records are available from extreme southeastern Campeche and central Petén, Guatemala (Porras et al. 2013). This individual was found at Nuevo Pochote, in the municipality of Emiliano Zapata, Tabasco (Charruau et al. 2014). Its EVS has been determined as 15 (Porras et al. 2013), placing it in the lower portion of the high vulnerability category (González-Sánchez et al. 2017). Its conservation status has been evaluated as Near Threatened (NT) by the IUCN and it has been allocated to the Special Protection (Pr) category by SEMARNAT. *Photo by Marco Antonio López-Luna.*

No. 35. *Crotalus tzabcan* Klauber, 1952. The Yucatan Neotropical Rattlesnake occurs in the Yucatan Peninsula, including Campeche, northeastern Chiapas, Quintana Roo, Tabasco, and Yucatán, México, northern Belize and El Petén, Guatemala (Lee 1996; Campbell 1998; Campbell and Lamar 2004). This individual was found in the village of El Triunfo in the municipality of Balancán, Tabasco. Its EVS has been determined as 16 (González-Sánchez et al. 2017), placing it in the middle portion of the high vulnerability category. Its conservation status has been designated as Least Concern (LC) by the IUCN, but as No Status (NS) by SEMARNAT. *Photo by Marco Antonio López-Luna.*

No. 36. *Metlapilcoatlus mexicanus* (Duméril, Bibron, and Duméril, 1854). The Central American Jumping Pitviper occurs at low, moderate, and intermediate elevations on the Atlantic slope “from southern Mexico through Central America south to Costa Rica and Panama, where it is also found on the Pacific versant” (Heimes 2016). This individual was found in the municipality of Tacotalpa, Tabasco, in secondary vegetation. Its EVS has been determined as 12 (Wilson et al. 2013a), placing it in the upper portion of the medium vulnerability category. Its conservation status has been assessed as Least Concern (LC) by the IUCN and it is allocated to the Threatened (A) category by SEMARNAT. *Photo by Marco Antonio López-Luna.*

Table 10. Summary of the distributional categories of the herpetofaunal families in Tabasco, Mexico, containing non-endemic species. The categorizations are as follows: MXUS, species distributed only in Mexico and the United States (except perhaps for a few also found in Canada); MXCA (species found only in Mexico and Central America); MXSA (species ranging from Mexico to South America); USCA (species ranging from the United States to Central America (except perhaps for a few also found in the Antilles); USSA (species ranging from the United States to South America); and OCEA (oceanic species).

Family	Number of non-endemic species	Distributional status					
		MXUS species (3)	MXCA species (4)	MXSA species (6)	USCA species (7)	USSA species (8)	OCEA species (9)
Bufonidae	3	—	2	—	1	—	—
Centrolenidae	1	—	1	—	—	—	—
Craugastoridae	4	—	4	—	—	—	—
Eleutherodactylidae	1	—	1	—	—	—	—
Hylidae	11	—	7	3	1	—	—
Leptodactylidae	3	—	—	2	—	1	—
Microhylidae	2	—	1	—	1	—	—
Phyllomedusidae	2	—	2	—	—	—	—
Ranidae	2	—	1	1	—	—	—
Rhinophrynidae	1	—	—	—	1	—	—
Subtotal	**30**	—	**19**	**6**	**4**	**1**	—
Plethodontidae	3	—	3	—	—	—	—
Subtotal	**3**	—	**3**	—	—	—	—
Dermophiidae	1	—	1	—	—	—	—
Subtotal	**1**	—	**1**	—	—	—	—
Total	**34**	—	**23**	**6**	**4**	**1**	—
Crocodylidae	2	—	1	—	—	1	—
Subtotal	**2**	—	**1**	—	—	**1**	—
Corytophanidae	4	—	3	1	—	—	—
Dactyloidae	10	—	9	1	—	—	—
Diploglossidae	1	—	1	—	—	—	—
Eublepharidae	1	—	1	—	—	—	—
Iguanidae	2	—	1	1	—	—	—
Mabuyidae	1	—	1	—	—	—	—
Phrynosomatidae	5	—	5	—	—	—	—
Phyllodactylidae	1	—	—	1	—	—	—
Scincidae	2	—	2	—	—	—	—
Sphaerodactylidae	2	—	2	—	—	—	—
Sphenomorphidae	1	—	1	—	—	—	—
Teiidae	2	—	1	1	—	—	—
Xantusiidae	1	—	1	—	—	—	—
Xenosauridae	1	—	1	—	—	—	—
Subtotal	**34**	—	**29**	**5**	—	—	—
Boidae	1	—	—	1	—	—	—
Colubridae	20	—	10	8	1	1	—
Dipsadidae	29	—	19	8	1	1	—
Elapidae	1	—	1	—	—	—	—
Leptotyphlopidae	1	—	1	—	—	—	—
Natricidae	3	1	—	—	2	—	—
Sibynophiidae	1	—	1	—	—	—	—
Typhlopidae	1	—	1	—	—	—	—
Viperidae	6	—	3	3	—	—	—
Subtotal	**63**	**1**	**36**	**20**	**4**	**2**	—
Cheloniidae	2	—	—	—	—	—	2
Chelydridae	1	—	1	—	—	—	—
Dermatemyidae	1	—	1	—	—	—	—
Dermochelyidae	1	—	—	—	—	—	1
Emydidae	1	—	—	1	—	—	—
Geoemydidae	1	—	1	—	—	—	—
Kinosternidae	3	—	1	2	—	—	—
Staurotypidae	2	—	2	—	—	—	—
Subtotal	**12**	—	**6**	**3**	—	—	**3**
Total	**111**	**1**	**72**	**28**	**4**	**3**	**3**
Sum total	**145**	**1**	**95**	**34**	**8**	**4**	**3**

Fig. 10. The human consumption of meat from iguanid lizards of the genus *Ctenosaura* documented in the municipality of Paraíso, Tabasco. *Photo by Liliana Ríos-Rodas.*

and crocodiles. Among the turtles, the species most affected are the Hicotea (*Trachemys venusta*), Pochitoque Tres Lomos (*Kinosternon scorpioides*), Pochitoque Jahuactero (*Kinosternon acutum*), and Chiquiguao (*Chelydra rossignonii*). Furthermore, the Lagarto or Cocodrilo (*Crocodylus moreletii*) and the Iguana Verde (*Iguana rhinolopha*) also are in frequent demand (Pozo-Montuy et al. 2019). The consumption of these species varies according to the region and season of the year. For instance, the consumption of freshwater turtles is a tradition for numerous Tabascan families during Lent.

Illegal Trade

Unfortunately, the illegal trafficking of reptile species in Tabasco is a common activity due to the high demand for meat (iguanas and crocodiles) and turtle eggs (Figs. 10–11). More specifically, many turtles in the state have been part of the Tabascan gastronomy (Guevara-Chumacero et al. 2017). Among turtles, people primarily eat *Dermatemys mawii* due to its size and meat quality, and consequently this consumption has pushed the species to near extinction (Zenteno-Ruíz et al. 2004). Although this species is consumed mostly in local communities, the species also is sold outside its distributional range, with prices varying according to the time of year (Guichard-Romero 2006). The crocodile (*C. moreletii*) is desired for its fat, since local communities use it for treating asthma. Furthermore, all of the species reported above often are purchased by people to keep as pets in tanks within their homes. With regard to amphibians, individuals of the treefrog *Agalychnis taylori* are sold as pets due to their attractive coloration, and often are advertised on websites by people lacking legal documentation. A similar situation is happening with the Central American Boa (*Boa imperator*), of which individuals usually are kept as pets, but also are sacrificed for their skin.

Fig. 11. Illegal trafficking of turtle species in the municipality of Centla, Tabasco. *Photo by Liliana Ríos-Rodas.*

Fig. 12. Forest fires caused by agricultural activities, Laguna San Isidro, Reserva de la Biosfera Pantanos de Centla, Tabasco. *Photo by Marco Antonio Torrez-Pérez.*

No. 37. *Dermatemys mawii* (Gray, 1847). The Central American River Turtle occurs in the Caribbean lowlands of southern Mexico from central Veracruz southeastward through the southern portion of the Yucatan Peninsula (Campbell 1998). In Tabasco this species is distributed practically throughout the state; however, wild populations have decreased considerably because it is hunted as a food source and its habitat has been severely modified (Rangel-Mendoza and Weber 2015). This individual belongs to the management unit of the Academic Division of Biological Sciences at the Universidad Juárez Autónoma de Tabasco. Its EVS has been determined as 17 (Wilson et al. 2013a), placing it in the middle portion of the high vulnerability category, and its IUCN status has been assessed as Critically Endangered (CR). It was allocated to the Endangered (P) category by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

No. 38. *Kinosternon leucostomum* (Duméril, Bibron, and Duméril, 1851). The White-lipped Mud Turtle occurs at low elevations from southern Veracruz, Mexico, southeastward through Central America to Colombia and the Pacific lowlands of Ecuador (Lee 1996). This individual was located at División Académica de Ciencias Biológicas of Universidad Juárez Autónoma de Tabasco, in the municipality of Centro. Wilson et al. (2013a) assessed its EVS as 10, placing it at the lower limit of the medium vulnerability category. Its conservation status has not been evaluated by the IUCN, but was assessed as Special Protection (Pr) by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

No. 39. *Claudius angustatus* Cope, 1865. The Narrow-bridged Musk Turtle occurs at low elevations on the Gulf versant of Mexico from southeastern Veracruz, Tabasco, and Campeche, and it is restricted to the base of the Península de Yucatán, through northern Guatemala and northern Belize (Lee 1996). This individual was located at División Académica de Ciencias Biológicas of Universidad Juárez Autónoma de Tabasco, in the municipality of Centro. Wilson et al. (2013a) assessed its EVS as 14, placing it at the lower limit of the high vulnerability category. Its conservation status was evaluated as Near Threatened (NT) by the IUCN, and it was placed in the Endangered (P) category by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

No. 40. *Staurotypus triporcatus* (Wiegmann, 1828). The Mexican Giant Musk Turtle occurs at low elevations on the Atlantic slope from central Veracruz, northern Oaxaca, northern and eastern Chiapas, western Campeche, Mexico, as well as southward and eastward through northern Guatemala and Belize (Lee 1996; Reynoso et al. 2016). This individual was located at División Académica de Ciencias Biológicas of Universidad Juárez Autónoma de Tabasco, in the municipality of Centro. Wilson et al. (2013a) assessed its EVS as 14, placing it at the lower limit of the high vulnerability category. Its conservation status has been evaluated as Near Threatened (NT) by the IUCN, and as Threatened (A) by SEMARNAT. *Photo by Liliana Ríos-Rodas.*

Wildfires

In general, farming activities cause most wild fires in Tabasco. The deliberate burning of grasses before cultivation is a frequent practice by farmers who burn the land to eliminate undesirable plants in order to benefit their grasslands. Furthermore, the resulting ashes from these fires are regarded as valuable fertilizer for their grasses (Cámara-Cabrales et al. 2019). Unfortunately, these practices are performed without any regulations, and may end up accidently burning a larger area than originally planned, including entire forest plantations (Cámara-Cabrales et al. 2019). In addition, remnant areas of tropical forest also are burned, since many farms are located within this vegetation type. Fires have caused communities such as Villa de Guadalupe in Huimanguillo, Sierra El Madrigal in Teapa, and Sierra de Tenosique, to eradicate large tracts of tropical forest, and consequently many animals are killed, impeded by their slow movement. Another important area that has suffered the consequences of wildfires is Reserva de la Biósfera Pantanos de Centla, where local villagers traditionally use fires to capture turtles during the dry season; and these fires not only kill the turtles, but also burn their nests and eggs (Beauregard-Solís et al. 2010; Zenteno-Ruíz et al. 2004).

Conservation Status

We used the same three systems of conservation assessment as in the previous entries in the Mexican Conservation Series (see above), i.e., SEMARNAT (2010), the IUCN Red List (http://iucnredlist.org), and the EVS (Wilson et al. 2013a, b). We have continued to update the assessments from these three systems as necessary.

The SEMARNAT System

The Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) of the federal government of Mexico developed a system of conservation assessment for the national fauna (SEMARNAT 2010), which is used by many Mexican herpetologists. Three categories are employed in the SEMARNAT system: endangered (P), threatened (A), and under special protection (Pr). We allocated the species remaining unassessed in this system to date into a "No Status" (NS) category. The ratings available for the Tabasco herpetofauna are given in Table 8 and summarized in Table 11.

As noted in previous entries in the Mexican Conservation Series (see above), only a small portion of the herpetofauna of Tabasco has been assessed using this system. Of the 165 native species occurring in Tabasco, only 56 species (33.9%) have been provided with SEMARNAT ratings and are placed in the three categories as follows: Endangered (P), four (2.4%); Threatened (A), 10 (6.1%); and Special Protection (Pr), 42 (25.5%). The majority of the species native to Tabasco (109, or 66.1%), however, have a No Status (NS) rating by the SEMARNAT system. In our opinion, until and unless all the species occurring in the state are assessed this system will be of little help in understanding the conservation needs of the herpetofauna of Tabasco.

Assuming that the SEMARNAT personnel have placed a greater emphasis on assessing endemic species in Mexico, then this should be evident by comparing the distributional category assignments and the SEMARNAT assessments. To ascertain whether such a bias exists, the pertinent data in Table 12 indicate that the majorities of species in Tabasco are non-endemic and have not been assessed (98, or 59.4%), and the evaluated species are also largely non-endemic (47, or 28.5%). Thus, these data indicate no bias toward the assessment of country endemic species.

The IUCN System

The system of conservation assessment developed and implemented by the International Union for Conservation of Nature is used broadly, but it has been criticized in earlier entries of the Mexican Conservation Series for several reasons, as discussed in Johnson et al. (2015b). Still, the assessments available for the Tabasco herpetofauna are collated in Table 8 and summarized in Table 13.

Of the 165 native herpetofaunal species in Tabasco, 114 (69.1%) have been evaluated using the IUCN system (Table 13). Of these 114 species, 19 have been allocated to the three threat categories of CR (four, or 3.5%); EN (four, or 3.5%); and VU (11, or 9.6%). The four CR species are the anurans *Ptychohyla macrotympanum* and *Agalychnis moreletii* and the turtles *Lepidochelys kempii* and *Dermatemys mawii*; and all four are non-endemic. The four EN species are the anurans *Charadrahyla chaneque* and *Duellmanohyla chamulae*, the salamander *Bolitoglossa veracrucis*, and the turtle *Chelonia mydas*; and the anurans and the salamander are country endemics while the turtle is non-endemic. The 11 VU species are the anurans *Incilius macrocristatus*, *Craugastor alfredi*, *C. rhodopis*, and *Eleutherodactylus leprus*, the salamander *Bolitoglossa alberchi*, the caecilian *Dermophis mexicanus*, the crocodylian *Crocodylus acutus*, the lizard *Norops barkeri*, and the turtles *Chelydra rossignonii*, *Dermochelys coriacea*, and *Trachemys venusta*. The three anurans are non-endemic, except for *C. rhodopis*, which is a country endemic, the salamander is a country endemic, the caecilian and crocodylian are non-endemic, the lizard is a country endemic, and the three turtles are non-endemic.

The remaining 95 species are placed in the "lower risk" categories of NT (10, or 6.1% of the total of 165 species) and LC (85, or 51.5%). The 10 NT species are the anurans *Craugastor berkenbuschii*, *C. laticeps*, *Rheohyla*

Table 11. SEMARNAT categorizations for the herpetofaunal species in Tabasco, Mexico, arranged by families. Non-native species are excluded.

Family	Number of species	SEMARNAT categorizations			
		Endangered (P)	Threatened (A)	Special protection (Pr)	No status (NS)
Bufonidae	3	—	—	—	3
Centrolenidae	1	—	—	—	1
Craugastoridae	7	—	—	2	5
Eleutherodactylidae	1	—	—	—	1
Hylidae	16	—	—	3	13
Leptodactylidae	3	—	—	—	3
Microhylidae	2	—	—	1	1
Phyllomedusidae	2	—	—	—	2
Ranidae	2	—	—	1	1
Rhinophrynidae	1	—	—	—	1
Subtotal	**38**	—	—	**7**	**31**
Plethodontidae	5	—	—	4	1
Subtotal	**5**	—	—	**4**	**1**
Dermophiidae	1	—	—	1	—
Subtotal	**1**	—	—	**1**	—
Total	**44**	—	—	**12**	**32**
Crocodylidae	2	—	—	2	—
Subtotal	**2**	—	—	**2**	—
Corytophanidae	4	—	—	3	1
Dactyloidae	13	—	—	3	10
Diploglossidae	1	—	—	1	—
Eublepharidae	1	—	1	—	—
Iguanidae	2	—	1	1	—
Mabuyidae	1	—	—	—	1
Phrynosomatidae	5	—	—	—	5
Phyllodactylidae	1	—	—	1	—
Scincidae	2	—	—	—	2
Sphaerodactylidae	2	—	—	1	1
Sphenomorphidae	2	—	—	1	1
Teiidae	5	—	—	—	5
Xantusiidae	2	—	1	1	—
Xenosauridae	1	—	—	—	1
Subtotal	**42**	—	**3**	**12**	**27**
Boidae	1	—	—	—	1
Colubridae	20	—	3	2	15
Dipsadidae	30	—	—	7	23
Elapidae	2	—	—	2	—
Leptotyphlopidae	1	—	—	—	1
Natricidae	3	—	2	—	1
Sibynophiidae	1	—	—	—	1
Typhlopidae	1	—	—	—	1
Viperidae	6	—	—	1	5
Subtotal	**65**	—	**5**	**12**	**48**
Cheloniidae	2	2	—	—	—
Chelydridae	1	—	—	—	1
Dermatemyidae	1	1	—	—	—
Dermochelyidae	1	1	—	—	—
Emydidae	1	—	—	—	1
Geoemydidae	1	—	1	—	—
Kinosternidae	3	—	—	3	—
Staurotypidae	2	—	1	1	—
Subtotal	**12**	**4**	**2**	**4**	**2**
Total	**121**	**4**	**10**	**30**	**77**
Sum total	**165**	**4**	**10**	**42**	**109**

Table 12. Comparison of the SEMARNAT and distributional categorizations for the Tabasco herpetofauna. Non-native species are excluded.

Distributional categories	SEMARNAT categories				
	Endangered (P)	Threatened (A)	Special Protection (Pr)	No Status (NS)	**Total**
Non-endemic species (NE)	4	9	34	98	**145**
Country-endemic species (CE)	—	1	9	10	**20**
Total	**4**	**10**	**43**	**108**	**165**

miotympanum, and *Smilisca cyanosticta* (two country endemics and two non-endemics), the salamander *Bolitoglossa platydactyla* (a country endemic), the lizard *Celestus rozellae* (a non-endemic), and the turtles *Rhinoclemmys areolata*, *Kinosternon acutum*, *Claudius angustatus*, and *Staurotypus triporcatus* (all non-endemics). The 85 LC species comprise the largest group of the native species (Table 13), but whether this large portion of the native species are in reality of "Least Concern" is a question we examine below.

Of the remaining 51 species in the herpetofauna, four are allocated to the DD category (2.4% of the total of 165 species) and 47 are in the NE category (28.5%). In the next section, we examine the status of these 51 species using the EVS system. To determine the relationship between the application of the IUCN categories and the distribution categories, the data on these correlations are assembled in Table 14. These data indicate that of the 20 country endemic species, six (30.0%) are allocated to the "threat categories." None of these six species is placed in the CR category, thus three species are in the EN category, including the anurans *Charadrahyla chaneque* and *Duellmanohyla chamulae*, and the salamander *Bolitoglossa veracrucis*. The other three species are consigned to the VU category, including the anuran *Craugastor rhodopis*, the salamander *Bolitoglossa alberchi*, and the anole *Norops barkeri*. The remaining CE species, numbering 14, are distributed rather uniformly among the other IUCN categories, with the highest number (five) placed in the LC category. As expected, the majority of the 145 non-endemic species (80, or 55.2%) are also allocated to the LC category. The next largest number (44, or 30.3%) was placed in the Not Evaluated (NE) category. The remaining non-endemic species (21, or 14.5%) are distributed among the remaining IUCN categories, with 13 placed in the "threat categories" (CR, EN, and VU). Based on the data in Table 14, no correlation is evident between the placements of the country endemic or non-endemic species among the IUCN's "threat categories." More to the point, as commonly found in earlier entries of the Mexican Conservation Series, most species of either distribution category (country endemic or non-endemic) are placed either in the LC category or are not assessed using the IUCN system. In the case of Tabasco, these species amount to 124 of the 145 non-endemic species (85.5%) and eight of the 20 country-endemic species (40.0%). In total, 132 of the 165 total native herpetofaunal species in Tabasco (80.0%) are placed either in the Least Concern or NE categories using the IUCN system. At this juncture, the IUCN assessment system has demonstrated that the majority of the evaluated herpetofauna is either of little concern (i.e., is in reasonably good shape from a conservation perspective) or simply has been ignored (i.e., non-evaluated). We further examine these LC and NE species in the next section.

The EVS System

The EVS (Environmental Vulnerability Score) system of conservation evaluation initially was created as a means for assessing the conservation status of the amphibians and reptiles of Honduras (Wilson and McCranie 2004). Subsequently, it has been used for the same purpose with other segments of the Mexican and Central American herpetofaunas (e.g., Townsend and Wilson 2010, 2013a,b; Johnson et al. 2015b, 2017; Mata-Silva et al. 2015, 2019; and all entries in the MCS [see above]). In this study, the EVS values for all 162 native non-marine species occurring in Tabasco are given in Table 8 and summarized in Table 15.

The EVS values range from 3 to 19, one less than the entire theoretical range of 3–20. The most frequent values (applied to 10 or more species) are 6 (13 species), 7 (12), 8 (13), 9 (16), 10 (21), 11 (16), 12 (15), 13 (17), 14 (11), and 15 (10). These 10 values are applied to 144 native non-marine species (88.9% of the total of 162 species). The lowest possible score of 3 was established for two anuran species (*Rhinella horribilis* and *Smilisca baudini*) and the highest score of 19 for one turtle (*Trachemys venusta*).

As with previous MCS reports, herein the EVS scores are aggregated into three categories of low (EVS of 3–9), medium (10–13), and high (14–19) vulnerability. On the basis of this categorization, the species counts increase slightly from low (66) to medium (69) and then decrease markedly to high (27). This sort of pattern is emblematic of herpetofaunas that contain more non-endemic species (145 in the case of Tabasco) than endemic species (20), as was previously determined in Chiapas (Johnson et al. 2015a), Tamaulipas (Terán-Juárez et al. 2016), Nuevo León (Nevárez-de los Reyes et al. 2016), Jalisco (Cruz-Sáenz et al. 2017), the Mexican Yucatan Peninsula (González-Sánchez et al. 2017), and Coahuila (Lazcano et al. 2019).

Table 13. IUCN Red List categorizations for the herpetofaunal families in Tabasco, Mexico. Non-native species are excluded. The shaded columns to the left are the "threat categories," and those to the right are the categories for which too little information on conservation status exists to allow the taxa to be placed in any other IUCN category, or they have not been evaluated.

Family	Number of species	IUCN Red List categorization						
		Critically Endangered (CR)	Endangered (EN)	Vulnerable (VU)	Near Threatened (NT)	Least Concern (LC)	Data Deficient (DD)	Not Evaluated (NE)
Bufonidae	3	—	—	1	—	1	—	1
Centrolenidae	1	—	—	—	—	1	—	—
Craugastoridae	7	—	—	2	2	1	2	—
Eleutherodactylidae	1	—	—	1	—	—	—	—
Hylidae	16	1	2	—	2	9	1	1
Leptodactylidae	3	—	—	—	—	3	—	—
Microhylidae	2	—	—	—	—	2	—	—
Phyllomedusidae	2	1	—	—	—	1	—	—
Ranidae	2	—	—	—	—	1	—	1
Rhinophrynidae	1	—	—	—	—	1	—	—
Subtotal	**38**	**2**	**2**	**4**	**4**	**20**	**3**	**3**
Plethodontidae	5	—	1	1	1	2	—	—
Subtotal	**5**	—	**1**	**1**	**1**	**2**	—	—
Dermophiidae	1	—	—	1	—	—	—	—
Subtotal	**1**	—	—	**1**	—	—	—	—
Total	**44**	**2**	**3**	**6**	**5**	**22**	**3**	**3**
Crocodylidae	2	—	—	1	—	1	—	—
Subtotal	**2**	—	—	**1**	—	**1**	—	—
Corytophanidae	4	—	—	—	—	4	—	—
Dactyloidae	13	—	—	1	—	1	—	11
Diploglossidae	1	—	—	—	1	—	—	—
Eublepharidae	1	—	—	—	—	1	—	—
Iguanidae	2	—	—	—	—	1	—	1
Mabuyidae	1	—	—	—	—	—	—	1
Phrynosomatidae	5	—	—	—	—	4	—	1
Phyllodactylidae	1	—	—	—	—	—	—	1
Scincidae	2	—	—	—	—	2	—	—
Sphaerodactylidae	2	—	—	—	—	1	—	1
Sphenomorphidae	2	—	—	—	—	1	—	1
Teiidae	5	—	—	—	—	3	—	2
Xantusiidae	2	—	—	—	—	1	1	—
Xenosauridae	1	—	—	—	—	—	—	1
Subtotal	**42**	—	—	**1**	**1**	**19**	**1**	**20**
Boidae	1	—	—	—	—	—	—	1
Colubridae	20	—	—	—	—	12	—	8
Dipsadidae	30	—	—	—	—	21	—	9
Elapidae	2	—	—	—	—	2	—	—
Leptotyphlopidae	1	—	—	—	—	—	—	1
Natricidae	3	—	—	—	—	3	—	—
Sibynophiidae	1	—	—	—	—	1	—	—
Typhlopidae	1	—	—	—	—	1	—	—
Viperidae	6	—	—	—	—	3	—	3
Subtotal	**65**	—	—	—	—	**43**	—	**22**
Cheloniidae	2	1	1	—	—	—	—	—
Chelydridae	1	—	—	1	—	—	—	—
Dermatemyidae	1	1	—	—	—	—	—	—
Dermochelyidae	1	—	—	1	—	—	—	—
Emydidae	1	—	—	1	—	—	—	—
Geoemydidae	1	—	—	—	1	—	—	—
Kinosternidae	3	—	—	—	1	—	—	2
Staurotypidae	2	—	—	—	2	—	—	—
Subtotal	**12**	**2**	**1**	**3**	**4**	—	—	**2**
Total	**121**	**2**	**1**	**5**	**5**	**63**	**1**	**44**
Sum total	**165**	**4**	**4**	**11**	**10**	**85**	**4**	**47**
Category total	**165**	**19**			**95**		**51**	

Table 14. Comparison of IUCN and distributional categorizations for the Tabasco herpetofauna. Non-native species are excluded.

Distributional categories	IUCN category							
	Critically Endangered (CR)	Endangered (EN)	Vulnerable (VU)	Near Threatened (NT)	Least Concern (LC)	Data Deficient (DD)	Not Evaluated (NE)	Total
Non-endemic species (NE)	4	1	8	7	80	1	44	**145**
Country-endemic species (CE)	—	3	3	3	5	3	3	**20**
Total	**4**	**4**	**11**	**10**	**85**	**4**	**47**	**165**

The results of applying the IUCN categories to the Tabasco herpetofauna are compared to those obtained from using the EVS system in Table 16. This comparison demonstrates that only 16 of the 27 high vulnerability species (59.3%) are placed in the three IUCN "threat categories." These 16 species are the anurans *Incilius macrocristatus* (VU 11), *Craugastor alfredi* (VU 11), *C. rhodopis* (VU 14), *Eleutherodactylus leprus* (VU 12), *Charadrahyla chaneque* (EN 13), *Duellmanohyla chamulae* (EN 13), *Ptychohyla macrotympanum* (CR 11), *Agalychnis moreletii* (CR 7), the salamanders *Bolitoglossa alberchi** (VU 15) and *Bolitoglossa veracrucis** (EN 17), the caecilian *Dermophis mexicanus* (VU 11), the crocodylian *Crocodylus acutus* (VU 14), the anole *Norops barkeri** (VU 15), and the turtles *Chelydra rossignonii* (VU 17), *Dermatemys mawii* (CR 17), and *Trachemys venusta* (VU 19). At the other extreme, the 65 low vulnerability species constitute 75.6% of the 86 LC species (Table 16). As demonstrated in the other MCS studies, there is a general lack of correspondence between the application of the IUCN and EVS assessment systems.

Only four of the 162 native non-marine species in the Tabasco herpetofauna are allocated to the DD category (Table 17), which are the anurans *Craugastor palenque*, *C. pelorus**, and *Exerodonta bivocata**, and the night lizard *Lepidophyma tuxtlae**. Based on similar arguments presented in previous MCS studies (e.g., Torres-Hernández et al. 2021), we suggest that the three anurans, each with an EVS of 15, would be better served by being placed in the EN category and the lizard, with an EVS of 11, in the NT category.

Forty-seven species still remain to be evaluated using the IUCN system, and thus we allocated them to the NE category (Tables 8 and 18). Only three of these species are country endemics (the anuran *Quilticohyla zoque* and the lizards *Holcosus amphigrammus* and *H. stuarti*). The remaining 44 species are all non-endemics. The EVS values range from 3–15, which allocates a certain number of species to each of the three summary categories (Table 8). Twenty-four species have a low EVS score, 19 have medium scores, and four have high scores. When these species are assessed by the IUCN, we suggest that the four high vulnerability species (*Quilticohyla zoque*, *Oxybelis potosiensis*, *Oxyrhopus petolarius*, and *Agkistrodon russeolus*), with an EVS of 14 or 15, should be placed in one of the three "threat categories." The 10 species with an EVS of 11, 12, or 13 should be allocated to the NT category. The remaining 33 species, with an EVS of 3–10, can be placed in the LC category.

As with all the previous entries in the Mexican Conservation Series, in this entry we ascertained that IUCN has placed a rather large segment of the Tabasco herpetofauna in the Least Concern category (Table 19). This includes 85 species, or 52.5% of the total of 162 native non-marine species. Since over half of the species in Tabasco have been judged by IUCN to be of Least Concern, one might conclude that the conservation status of this herpetofauna is in reasonably good shape. To examine whether this is the case, the determinations of the EVS values for these 85 species are shown in Table 19. Given that the majority of the Tabasco herpetofauna is comprised of non-endemic species, one might expect that a large portion of these species should be assigned to the LC category, which proves to be the case. Only five (5.9%) of these LC species are country endemics. The EVS values for the 85 LC species range from 3 to 17, or only three fewer than the entire theoretical range for the EVS (i.e., 3–20). This range is two fewer than the entire range for Tabasco (3–19). Allocation of the EVS values for the 85 LC species into the three summary categories indicates the following: low (3–9), 40 species; medium (10–13), 38 species; and high (14–20), 7 species. On the basis of these allocations, we suggest that a more realistic evaluation would position the seven high vulnerability species in one of the three threat categories, as: CR (*Micrurus diastema*); EN (*Crotalus tzabcan*); and VU (*Triprion spinosus*, *Norops compressicauda*, *Sceloporus lundelli*, *Dipsas brevifacies*, and *Porthidium nasutum*). The 40 medium vulnerability species most logically should be allocated to the NT category, and the 40 low vulnerability species should be retained in the LC category, at least until more up-to-date, targeted conservation status surveys can be completed.

Relative Herpetofaunal Priority

Johnson et al. (2015a) developed the concept of Relative Herpetofaunal Priority (RHP) in the third entry of the MCS. This device is a simple means for measuring the

Table 15. Environmental Vulnerability Scores (EVS) for the herpetofaunal species in Tabasco, Mexico, arranged by family. The shaded area to the left encompasses low vulnerability scores, and the one to the right indicates the high vulnerability scores. Non-native species are excluded.

Family	Number of species	Environmental Vulnerability Score																
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Bufonidae	3	1	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—
Centrolenidae	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Craugastoridae	7	—	—	—	—	—	—	—	1	1	1	—	2	2	—	—	—	—
Eleutherodactylidae	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Hylidae	16	1	2	—	—	2	1	1	2	1	1	2	2	1	—	—	—	—
Leptodactylidae	3	—		1	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Microhylidae	2	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Phyllomedusidae	2	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—
Ranidae	2	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—
Rhinophrynidae	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Subtotal	**38**	**2**	**3**	**1**	**2**	**4**	**4**	**2**	**4**	**4**	**3**	**2**	**4**	**3**	—	—	—	—
Plethodontidae	5	—	—	—	—	—	—	1	—	1	—	—	—	2	—	1	—	—
Subtotal	**5**	—	—	—	—	—	—	**1**	—	**1**	—	—	—	**2**	—	**1**	—	—
Dermophiidae	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Subtotal	**1**	—	—	—	—	—	—	—	—	**1**	—	—	—	—	—	—	—	—
Total	**44**	**2**	**3**	**1**	**2**	**4**	**4**	**3**	**4**	**6**	**3**	**2**	**4**	**5**	—	**1**	—	—
Crocodylidae	2	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—
Subtotal	**2**	—	—	—	—	—	—	—	—	—	—	**1**	**1**	—	—	—	—	—
Corytophanidae	4	—	—	—	—	1	—	1	—	1	—	1	—	—	—	—	—	—
Dactyloidae	13	—	—	—	—	1	2	3	2	—	1	2	—	2	—	—	—	—
Diploglossidae	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Eublepharidae	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Iguanidae	2	—	—	—	—	—	1		—	—	1	—	—	—	—	—	—	—
Mabuyidae	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Phrynosomatidae	5	—	—	1	1	—	—	—	—	—	—	2	1	—	—	—	—	—
Phyllodactylidae	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Scincidae	2	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—
Sphaerodactylidae	2	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—
Sphenomorphidae	2	—	—	—	—	1	—	—	—	1		—	—	—	—	—	—	—
Teiidae	5	—	—	—	—	—	1	—	—	2	2	—	—	—	—	—	—	—
Xantusiidae	2	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—
Xenosauridae	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Subtotal	**42**	—	—	**1**	**2**	**3**	**5**	**5**	**4**	**7**	**6**	**6**	**1**	**2**	—	—	—	—
Boidae	1	—	—	—	—	—	—	—	1	—	—		—	—	—	—	—	—
Colubridae	20	—	—	1	7	1	1	4	3	—	1	1	—	1	—	—	—	—
Dipsadidae	30	—	1	2	2	3	3	4	5	2	2	4	1	1	—	—	—	—
Elapidae	2	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—
Leptotyphlopidae	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Natricidae	3	—	—	—	—	1	—	—	2	—	—	—	—	—	—	—	—	—
Sibynophiidae	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Typhlopidae	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Viperidae	6	—	—	—	—	—	—	—	—	—	2	1	1	1	1	—	—	—
Subtotal	**65**	—	**2**	**3**	**9**	**5**	**4**	**8**	**11**	**3**	**6**	**7**	**2**	**3**	**1**	**1**	—	—
Chelydridae	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Dermatemyidae	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Emydidae	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Geoemydidae	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Kinosternidae	3	—	—	—	—	—	—	—	2	—	—	—	1	—	—	—	—	—
Staurotypidae	2	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
Subtotal	**9**	—	—	—	—	—	—	—	**2**	—	—	**1**	**3**	—	—	**2**	—	**1**
Total	**118**	—	**2**	**4**	**11**	**8**	**9**	**13**	**17**	**10**	**12**	**15**	**7**	**5**	**1**	**3**	—	**1**
Sum total	**162**	**2**	**5**	**5**	**13**	**12**	**13**	**16**	**21**	**16**	**15**	**17**	**11**	**10**	**1**	**4**	—	**1**
Category total	**162**	**66**							**69**				**27**					

Table 16. Comparison of Environmental Vulnerability Scores (EVS) and IUCN categorizations for members of the herpetofauna of Tabasco, Mexico. Non-native species and marine species are excluded. The shaded area at the top encompasses low vulnerability category scores, and the one at the bottom includes the high vulnerability category scores.

EVS	IUCN category							
	Critically Endangered	Endangered	Vulnerable	Near Threatened	Least Concern	Data Deficient	Not Evaluated	Total
3	—	—	—	—	1	—	1	2
4	—	—	—	—	4	—	1	5
5	—	—	—	—	2	—	3	5
6	—	—	—	—	8	—	4	12
7	1	—	—	—	7	—	4	12
8	—	—	—	—	9	—	4	13
9	—	—	—	1	9	—	7	17
10	—	—	—	—	13	—	9	22
11	1	—	3	—	9	1	2	16
12	—	—	1	2	7	—	4	14
13	—	2	—	2	9	—	4	17
14	—	—	2	4	3	—	2	11
15	—	—	2	1	2	3	2	10
16	—	—	—	—	1	—	—	1
17	1	1	1	—	1	—	—	4
19	—	—	1	—	—	—	—	1
Total	**3**	**3**	**10**	**10**	**85**	**4**	**47**	**162**

relative importance of the herpetofaunal components of the physiographic regions in any given geographic entity, such as states in Mexico in the case of the MCS. Ascertaining the RHP is accomplished by using two metrics, i.e., (1) the proportions of state and country endemics (only country endemics in the case of Tabasco) among the physiographic regional herpetofaunas, and (2) the absolute quantity of high vulnerability category species in each physiographic regional herpetofauna. The data resulting from these calculations are presented in Tables 20 and 21, respectively.

The data in Table 20 are based on the relative number of country endemics (since there are no state endemic species in Tabasco). These data demonstrate that the first rank is occupied by the SNC with 17 species of a total of 145 species (11.7%). The second rank is held by the GCP with five country endemics among a total of 89 species (5.6%), and the third rank is the SBP with three country endemics among a total of 93 species (3.2%).

The data in Table 21 show the relative numbers of high vulnerability species, but the rankings differ somewhat from those seen in Table 20. The first rank is the same in both instances, i.e., the Sierra Norte de Chiapas, with 23 high vulnerability species among a total of 142 species (16.2%). The second rank relative to the high vulnerability species, however, is held by the Sierras Bajas de Petén with 15 such species among a total of 91 (16.5%), although it holds rank number three with respect to country endemics. The third rank in Table 21 is for the Gulf Coastal Plain, with 10 high vulnerability species among a total of 79 (12.7%), while this region's status is rank two relative to country endemics.

Based on the results of the RHP analyses, the physiographic region with the highest priority is clearly the SNC, since it supports the highest numbers of both country endemics (Table 20) and high vulnerability species (Table 21). The 17 country endemics, as indicated by the asterisks in Table 4, include eight anurans (*Craugastor berkenbuschii*, *C. pelorus*, *C. rhodopis*, *Charadrahyla chaneque*, *Duellmanohyla chamulae*, *Exerodonta bivocata*, *Quilticohyla zoque*, and *Rheohyla miotympanum*), two salamanders (*Bolitoglossa*

Table 17. Environmental Vulnerability Scores (EVS) for members of the herpetofauna of Tabasco, Mexico, allocated to the IUCN Data Deficient category. * = country endemic.

Species	Environmental Vulnerability Score (EVS)			
	Geographic distribution	Ecological distribution	Reproductive mode/Degree of persecution	Total score
Craugastor palenque	4	7	4	15
*Craugastor pelorus**	5	6	4	15
*Exerodonta bivocata**	6	8	1	15
*Lepidophyma tuxtlae**	5	4	2	11

Table 18. Environmental Vulnerability Scores (EVS) for members of the herpetofauna of Tabasco, Mexico, currently Not Evaluated (NE) by the IUCN. Non-native species are excluded. * = country endemic.

Species	Environmental Vulnerability Score (EVS)			
	Geographic distribution	Ecological distribution	Reproductive mode/Degree of persecution	Total score
Rhinella horribilis	1	1	1	3
*Quilticohyla zoque**	5	8	1	14
Lithobates brownorum	4	3	1	8
Norops beckeri	3	6	3	12
Norops biporcatus	3	4	3	10
Norops capito	3	7	3	13
Norops laeviventris	3	3	3	9
Norops lemurinus	3	2	3	8
Norops petersi	2	4	3	9
Norops rodriguezii	4	3	3	10
Norops sericeus	2	3	3	8
Norops tropidonotus	4	2	3	9
Norops uniformis	4	6	3	13
Norops unilobatus	1	3	3	7
Iguana rhinolopha	1	3	6	10
Marisora lineola	4	3	3	10
Sceloporus variabilis	1	1	3	5
Thecadactylus rapicauda	3	4	3	10
Sphaerodactylus continentalis	4	3	3	10
Scincella cherriei	3	2	3	8
*Holcosus amphigrammus**	5	3	3	11
*Holcosus stuarti**	5	4	3	12
Xenosaurus rackhami	4	4	3	11
Boa imperator	3	1	6	10
Drymobius margaritiferus	1	1	4	6
Lampropeltis polyzona	1	1	6	8
Leptophis ahaetulla	3	3	4	10
Oxybelis fulgidus	3	2	4	9
Oxybelis potosiensis	5	7	3	15
Spilotes pullatus	1	1	4	6
Stenorrhina degenhardtii	3	3	3	9
Stenorrhina freminvillii	1	2	4	7
Coniophanes fissidens	1	3	3	7
Enulius flavitorques	1	1	3	5
Imantodes cenchoa	1	3	2	6
Imantodes gemmistratus	1	3	2	6
Leptodeira septentrionalis	2	2	4	8
Oxyrhopus petolarius	3	6	5	14
Rhadinaea decorata	1	6	2	9
Sibon nebulatus	1	2	2	5
Xenodon rabdocephalus	3	5	5	13
Epictia phenops	1	4	1	6
Agkistrodon russeolus	4	6	5	15
Bothriechis schlegelii	2	6	5	13
Bothrops asper	3	4	5	12
Kinosternon leucostomum	3	4	3	10
Kinosternon scorpioides	3	4	3	10

Table 19. Environmental Vulnerability Scores (EVS) for members of the herpetofauna of Tabasco, Mexico, assigned to the IUCN Least Concern (LC) category. Non-native species are excluded. * = country endemic.

Species	Environmental Vulnerability Score (EVS)			
	Geographic distribution	Ecological distribution	Reproductive mode/Degree of persecution	Total score
Incilius valliceps	3	2	1	6
Hyalinobatrachium viridissimum	3	4	3	10
Craugastor loki	2	4	4	10
Dendrosophus ebraccatus	3	6	1	10
Dendrosophus microcephalus	3	3	1	7
Scinax staufferi	2	1	1	4
Smilisca baudinii	1	1	1	3
Tlalocohyla loquax	3	3	1	7
Tlalocohyla picta	2	5	1	8
Trachycephalus vermiculatus	1	2	1	4
Triprion petasatus	4	5	1	10
Triprion spinosus	3	6	5	14
Engystomops pustulosus	3	2	2	7
Leptodactylus fragilis	1	2	2	5
Leptodactylus melanonotus	1	3	2	6
Gastrophryne elegans	2	5	1	8
Hypopachus variolosus	2	1	1	4
Agalychnis taylori	3	5	3	11
Lithobates vaillanti	3	5	1	9
Rhinophrynus dorsalis	2	5	1	8
Bolitoglossa mexicana	4	3	4	11
Bolitoglossa rufescens	1	4	4	9
Crocodylus moreletii	2	5	6	13
Basiliscus vittatus	1	3	3	7
Corytophanes cristatus	3	5	3	11
Corytophanes hernandezii	4	6	3	13
Laemanctus longipes	1	5	3	9
*Norops compressicauda**	5	7	3	15
Coleonyx elegans	2	3	4	9
Ctenosaura similis	1	4	3	8
Sceloporus chrysostictus	4	6	3	13
Sceloporus lundelli	4	7	3	14
Sceloporus serrifer	2	1	3	6
Sceloporus teapensis	4	6	3	13
Mesoscincus schwartzei	2	6	3	11
Plestiodon sumichrasti	4	5	3	12
Sphaerodactylus glaucus	4	5	3	12
*Scincella gemmingeri**	5	3	3	11
Aspidoscelis deppii	1	4	3	8
*Aspidoscelis guttatus**	5	4	3	12
Holcosus festivus	3	5	3	11
Lepidophyma flavimaculatum	1	5	2	8
Dendrophidion vinitor	3	7	3	13
Drymarchon melanurus	1	1	4	6
Ficimia publia	4	3	2	9
Leptophis mexicanus	1	1	4	6
Masticophis mentovarius	1	1	4	6
Mastigodryas melanolomus	1	1	4	6
Phrynonax poecilonotus	3	4	3	10
Pseudelaphe flavirufa	2	4	4	10

Table 19 (continued). Environmental Vulnerability Scores (EVS) for members of the herpetofauna of Tabasco, Mexico, assigned to the IUCN Least Concern (LC) category. Non-native species are excluded. * = country endemic.

Species	Environmental Vulnerability Score (EVS)			
	Geographic distribution	Ecological distribution	Reproductive mode/Degree of persecution	Total score
Senticolis triaspis	2	1	3	6
Tantilla rubra	2	1	2	5
Tantilla schistosa	3	3	2	8
Tantillita lintoni	4	6	2	12
Adelphicos quadrivirgatum	4	4	2	10
Amastridium sapperi	4	4	2	10
Clelia scytalina	4	5	4	13
Coniophanes bipunctatus	1	5	3	9
Coniophanes imperialis	2	3	3	8
Coniophanes piceivittis	1	3	3	7
Coniophanes quinquevittatus	4	6	3	13
Coniophanes schmidti	4	6	3	13
Conophis lineatus	2	3	4	9
Dipsas brevifacies	4	7	4	15
Geophis carinosus	2	4	2	8
*Geophis laticinctus**	5	4	2	11
Geophis sanniolus	4	6	2	12
Geophis sartorii	2	2	5	9
Leptodeira frenata	4	4	4	12
Leptodeira maculata	2	1	4	7
Ninia diademata	4	3	2	9
Ninia sebae	1	2	2	5
Pliocercus elapoides	4	1	5	10
Sibon dimidiatus	1	5	4	10
Tretanorhinus nigroluteus	3	5	2	10
*Micrurus diastema**	5	7	5	17
Micrurus elegans	4	4	5	13
Nerodia rhombifer	1	5	4	10
Thamnophis marcianus	1	5	4	10
Thamnophis proximus	1	2	4	7
Scaphiodontophis annulatus	1	5	5	11
Amerotyphlops tenuis	4	7	1	12
Crotalus tzabcan	4	7	5	16
Metlapilcoatlus mexicanus	3	4	5	12
Porthidium nasutum	3	6	5	14

platydactyla and *B. veracrucis*), five lizards (*Norops barkeri*, *N. compressicauda*, *Holcosus amphigrammus*, *H. stuarti*, and *Lepidophyma tuxtlae*), and two snakes (*Geophis laticinctus* and *Micrurus diastema*). The 23 high vulnerability species found in the SNC are identified in Table 8 and are listed here for emphasis:

*Craugastor berkenbuschii**
Craugastor palenque
*Craugastor pelorus**
*Craugastor rhodopis**
*Exerodonta bivocata**
*Quilticohyla zoque**
Triprion spinosus
*Bolitoglossa platydactyla**
*Bolitoglossa veracrucis**
Crocodylus acutus
*Norops barkeri**
*Norops compressicauda**
Sceloporus lundelli
Oxybelis potosiensis
Dipsas brevifacies
Oxyrhopus petolarius
*Micrurus diastema**
Porthidium nasutum
Chelydra rossignonii
Dermatemys mawii
Trachemys venusta
Kinosternon acutum
Staurotypus triporcatus

Table 20. Number of herpetofaunal species in the three distributional status categories among the three physiographic regions of Tabasco, Mexico. Rank order is based on the number of country endemics.

Physiographic region	Distributional categories			Total	Rank order
	Non-endemics	Country Endemics	Non-natives		
Gulf Coastal Plain	78	5	5	88	2
Sierra Norte de Chiapas	125	17	3	145	1
Sierras Baja del Petén	88	3	2	93	3

Of these 23 species, 10 are country endemics (*) with EVS values ranging from 14 to 19.

The GCP includes five country endemics: the anuran *Craugastor rhodopis*, the lizards *Aspidoscelis guttatus*, *Holcosus amphigrammus*, and *H. stuarti*, and the snake *Micrurus diastema*. The GCP also harbors 10 high vulnerability species, which are indicated in Table 8 and listed here for emphasis:

*Craugastor rhodopis**
Crocodylus acutus
Oxybelis potosiensis
*Micrurus diastema**
Chelydra rossignonii
Dermatemys mawii
Trachemys venusta
Kinosternon acutum
Claudius angustatus
Staurotypus triporcatus

Only two of these 10 species are country endemics (*), but the EVS values for all ten range from 14 to 19.

Finally, the SBP contains only three country endemics: the anuran *Craugastor rhodopis*, the salamander *Bolitoglossa alberchi*, and the lizard *Scincella gemmingeri*. This region, however, supports 15 high vulnerability species that are listed in Table 8 and here for emphasis:

Craugastor palenque
*Craugastor rhodopis**
*Bolitoglossa alberchi**
Crocodylus acutus
Sceloporus lundelli
Oxybelis potosiensis
Agkistrodon russeolus
Crotalus tzabcan
Porthidium nasutum
Chelydra rossignonii
Dermatemys mawii
Trachemys venusta
Kinosternon acutum
Claudius angustatus
Staurotypus triporcatus

Only two of these 15 species are country endemics (*), but the EVS values for all 15 species range from 14 to 19.

In each of the three physiographic regions we recognize in Tabasco, the largest distributional group, as expected, is comprised of the non-endemic species. Similarly, the high vulnerability species in each region are non-endemic species. As a result, unlike the many states surveyed thus far in the MCS, the group of principal conservation concern in Tabasco is the non-endemic segment. Consequently, this group of species is examined more closely below in an effort to protect the herpetofauna of Tabasco.

Natural Protected Areas in Tabasco

The ostensible purpose for the establishment of natural protected areas in any location is to protect key portions of the ecosystems contained within them from the depredations of societal elements outside them for perpetuity. Basically, there are two types of issues, i.e., agriculturalization and urbanization. To be maximally effective, such protected areas should include functionally capable segments of the ecosystems originally present in a given entity (e.g., a state), whose size and extent is sufficient to support viable populations of all the organisms found within the designated protected area. Most often, however, such areas are established without the completion of the requisite work to demonstrate the existence of survivable populations of anything more than a handful of the resident creatures. When

Table 21. Number of herpetofaunal species in the three EVS categories among the three physiographic regions of Tabasco, Mexico. Rank order is determined by the relative number of high EVS species. Non-native and marine species are excluded.

Physiographic province	Low	Medium	High	Total	Rank order
Gulf Coastal Plain	39	31	10	79	3
Sierra Norte de Chiapas	60	59	23	142	1
Sierras Baja del Petén	38	38	15	91	2

Table 22. Characteristics of Natural Protected Areas in Tabasco, Mexico. Abbreviations in Facilities available are as follows: A = administrative services; R = park guards; S = system of pathways; and V = facilities for visitors. Category abbreviations: RB= Reserva de la Biósfera; APFF= Área de Protección de Flora y Fauna; PE= Parque Estatal; CICN= Centro de Integración y Conocimiento de la Naturaleza; RE= Reservas estatales; MN= Monumento Natural; and ADVC= Áreas destinadas voluntariamente a la conservación. The two data sources consulted were: (i) Ávalos-Lázaro AA, Bautista-López SA y Martínez-Rivera AK. 2010. Composición y estructura de la comunidad herpetofaunistica en la temporada de estiaje del ANP Yumká en Villahermosa, Tabasco. XI Reunión Nacional de Herpetología. Programa y Resúmenes. Sociedad Herpetológica Mexicana, UAEM. Toluca, Estado de México; and (ii) Secretaría de Bienestar, Sustentabilidad y Cambio Climático (SBSCC). 2019. Listado de áreas Naturales Protegidas. Sistema Estatal de Áreas Naturales Protegidas, https://tabasco.gob.mx/areas-naturales-protegidas-tabasco, Accessed: 30 July 2021.

Name	Category	Date of Decree (dd/mm/yyyy)	Area (ha)	Municipalities	Jurisdiction	Physiographic region	Facilities available	Occupied by landowners	Management plan available	Herpetofaunal survey completed
Pantanos de Centla	Reserva de la Biósfera	06/08/1992	302,707	Centla, Jonuta and Macuspana	Mexican federal government	Llanura Costera del Golfo Sur	A,R,S,V	Yes	Yes	Yes
Cañón del Usumacinta	APFF	22/09/2008	46,128	Tenosique	Mexican federal government	Sierras Bajas del Petén	S,V	Yes	Yes	No
Agua Blanca	PE	19/12/1987	2,025	Macuspana	State	Llanura Costera del Golfo Sur	A,R,S,V	Yes	Yes	Yes
La Sierra de Tabasco	PE	24/02/1988	15,113.2	Tacotalpa, Teapa	State	Sierras del Norte de Chiapas	R,S	Yes	No	No
Laguna del Camarón	PE	19/12/2012	83	Centro	State	Llanura Costera del Golfo Sur	S	Yes	No	Yes
CICN Yumká	RE	19/12/1998	101	Centro	State	Llanura Costera del Golfo Sur	A,R,S,V	No	No	Yes
Reserva Ecológica de la Chontalpa	RE	08/02/1995	277	Cárdenas	State	Llanura Costera del Golfo Sur	A,R,S,V	No	No	No
Laguna de las Ilusiones	RE	08/02/1995	259.3	Centro	State	Llanura Costera del Golfo Sur	A,R,S,V	No	Yes	Yes
Yu-Balcah	RE	10/06/2000	572	Tacotalpa	State	Sierras del Norte de Chiapas	A,R,S,V	No	No	No
Cascadas de Reforma	RE	23/11/2002	5,748.4	Balancán	State	Llanura Costera del Golfo Sur	S,V	Yes	No	No
Río Playa	RE	29/09/2004	711	Centla	State	Llanura Costera del Golfo Sur	A,S	Yes	No	No
Grutas del Cerro Coconá	MN	24/02/1988	442	Teapa	State	Sierras del Norte de Chiapas	A,R,S,V	Yes	No	Yes
Laguna Mecoacán	PE	25/09/2019	18,774.7	Jalpa de Méndez, Paraíso	State	Llanura Costera del Golfo Sur	S,V	Yes	No	No
Guaritec	ADVC	10/07/2014	7	Centla	Private	Llanura Costera del Golfo Sur	A,R,S,V	No	Yes	No

Table 23. Distribution of herpetofaunal species in the Natural Protected Areas of Tabasco, Mexico, based on herpetofaunal surveys. Abbreviations are as follows: * = species endemic to Mexico and ** = non-native species. The numbers signifying the 14 Natural Protected Areas in Tabasco are as follows: 1 = Pantanos de Centla; 2 = Cañon del Usumacinta; 3 = Agua Blanca; 4 = La Sierra de Tabasco; 5 = Laguna del Camarón; 6 = CICN Yumká; 7 = Reserva Ecológico de la Chontalpa; 8 = Laguna de las Ilusiones; 9 = Yu-Balcah; 10 = Cascadas de Reforma; 11 = Río Playa; 12 = Grutas del Cerro Coconá; 13 = Laguna Mecoacán; and 14 = Guaritec.

Taxon	Natural Protected Area													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Anura (38 species)														
Bufonidae (3 species)														
Incilius valliceps	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Incilius macrocristatus				+								+		
Rhinella horribilis	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Centrolenidae (1 species)														
Hyalinobatrachium viridissimum	+			+										
Craugastoridae (7 species)														
Craugastor alfredi		+	+	+					+			+		
*Craugastor berkenbuschii**			+											
Craugastor laticeps			+	+					+			+		
Craugastor loki				+								+		
Craugastor palenque		+												
*Craugastor pelorus**			+	+										
*Craugastor rhodopis**		+	+	+					+			+		
Eleutherodactylidae (2 species)														
Eleutherodactylus leprus		+	+	+								+		
*Eleutherodactylus planirostris***							+							
Hylidae (15 species)														
*Charadrahyla chaneque**				+										
Dendrosophus ebraccatus														
Dendrosophus microcephalus	+	+		+				+	+			+		+
*Duellmanohyla chamulae**				+										
*Exerodonta bivocata**				+										
Ptychohyla macrotympanum				+										
*Quilticohyla zoque**				+										
*Rheohyla miotympanum**														
Scinax staufferi	+	+	+	+		+	+	+	+	+	+	+	+	+
Smilisca baudinii	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Smilisca cyanosticta		+	+	+										
Tlalocohyla loquax	+			+	+	+	+	+	+	+	+	+	+	+
Tlalocohyla picta	+			+				+				+		+
Trachycephalus vermiculatus	+	+		+				+	+			+	+	
Triprion petasatus				+										
Triprion spinosus				+								+		
Leptodactylidae (3 species)														
Engystomops pustulosus		+								+				
Leptodactylus fragilis	+	+		+			+	+					+	
Leptodactylus melanonotus	+	+	+	+								+		
Microhylidae (2 species)														
Gastrophyrne elegans				+								+		

Table 23 (continued). Distribution of herpetofaunal species in the Natural Protected Areas of Tabasco, Mexico, based on herpetofaunal surveys. Abbreviations are as follows: * = species endemic to Mexico and ** = non-native species. The numbers signifying the 14 Natural Protected Areas in Tabasco are as follows: 1 = Pantanos de Centla; 2 = Cañon del Usumacinta; 3 = Agua Blanca; 4 = La Sierra de Tabasco; 5 = Laguna del Camarón; 6 = CICN Yumká; 7 = Reserva Ecológico de la Chontalpa; 8 = Laguna de las Ilusiones; 9 = Yu-Balcah; 10 = Cascadas de Reforma; 11 = Río Playa; 12 = Grutas del Cerro Coconá; 13 = Laguna Mecoacán; and 14 = Guaritec.

Taxon	**Natural Protected Area**													
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Hypopachus variolosus	+	+												
Phyllomedusidae (2 species)														
Agalychnis moreletii														
Agalychnis callidryas	+	+		+										
Ranidae (2 species)														
Lithobates brownorum	+			+	+			+		+	+	+	+	+
Lithobates vaillanti	+	+	+	+					+	+			+	+
Rhinophrynidae (1 species)														
Rhinophrynus dorsalis	+			+	+	+	+	+			+		+	+
Caudata (5 species)														
Plethodontidae (5 species)														
*Bolitoglossa alberchi**		+												
Bolitoglossa mexicana		+		+								+		
*Bolitoglossa platydactyla**				+										
Bolitoglossa rufescens				+										
*Bolitoglossa veracrucis**														
Gymnophiona (1 species)														
Dermophiidae (1 species)														
Dermophis mexicanus	+							+			+	+	+	
Reptilia (124 species)														
Crocodylia (2 species)														
Crocodylidae (2 species)														
Crocodylus acutus		+				+								
Crocodylus moreletii	+	+			+	+		+			+		+	
Squamata (110 species)														
Corytophanidae (4 species)														
Basiliscus vittatus	+	+	+	+						+	+	+	+	+
Corytophanes cristatus				+								+		
Corytophanes hernandezii		+	+	+								+		
Laemanctus longipes	+	+		+					+	+				
Dactyloidae (14 species)														
*Norops barkeri**		+	+	+								+		
Norops beckeri			+	+										
Norops biporcatus			+	+										
Norops capito				+								+		
*Norops compressicauda**				+								+		
Norops laeviventris												+		
Norops lemurinus	+	+	+	+		+	+	+	+	+	+	+	+	
Norops rodriguezii		+	+	+								+		
*Norops sagrei***	+	+	+		+	+	+	+		+	+	+		

Table 23 (continued). Distribution of herpetofaunal species in the Natural Protected Areas of Tabasco, Mexico, based on herpetofaunal surveys. Abbreviations are as follows: * = species endemic to Mexico and ** = non-native species. The numbers signifying the 14 Natural Protected Areas in Tabasco are as follows: 1 = Pantanos de Centla; 2 = Cañon del Usumacinta; 3 = Agua Blanca; 4 = La Sierra de Tabasco; 5 = Laguna del Camarón; 6 = CICN Yumká; 7 = Reserva Ecológico de la Chontalpa; 8 = Laguna de las Ilusiones; 9 = Yu-Balcah; 10 = Cascadas de Reforma; 11 = Río Playa; 12 = Grutas del Cerro Coconá; 13 = Laguna Mecoacán; and 14 = Guaritec.

Taxon	Natural Protected Area													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Norops sericeus	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Norops tropidonotus		+	+	+					+			+		
Norops petersii				+								+		
Norops uniformis		+	+	+								+		
Norops unilobatus		+												
Diploglossidae (1 species)														
Celestus rozellae												+		
Eublepharidae (1 species)														
Coleonyx elegans		+	+	+		+						+	+	
Gekkonidae (2 species)														
*Hemidactylus frenatus***	+	+	+	+	+	+	+	+	+	+	+	+	+	+
*Hemidactylus turcicus***	+	+					+			+		+	+	
Iguanidae (2 species)														
Ctenosaura similis	+	+		+				+	+	+			+	
Iguana rhinolopha	+	+	+	+	+	+	+	+		+	+	+	+	+
Mabuyidae (1 species)														
Marisora lineola	+				+	+	+	+					+	+
Phrynosomatidae (5 species)														
Sceloporus chrysostictus	+	+								+				
Sceloporus lundelli		+	+											
Sceloporus serrifer		+	+									+		
Sceloporus teapensis		+		+								+		
Sceloporus variabilis	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Phyllodactylidae (1 species)														
Thecadactylus rapicauda		+	+											
Scincidae (2 species)														
Mesoscincus schwartzei	+	+	+						+					
Plestiodon sumichrasti	+		+	+								+		
Sphaerodactylidae (2 species)														
Sphaerodactylus glaucus	+	+		+										
Sphaerodactylus millepunctatus		+		+										
Sphenomorphidae (2 species)														
Scincella cherriei	+	+	+	+								+		
*Scincella gemmingeri**			+											
Teiidae (5 species)														
Aspidoscelis deppii	+		+										+	
*Aspidoscelis guttatus**		+												
*Holcosus amphigrammus**	+	+	+	+						+		+	+	
Holcosus festivus	+	+	+	+				+						
*Holcosus stuarti**	+			+						+				
Holcosus undulatus	+	+	+	+			+			+		+	+	

Table 23 (continued). Distribution of herpetofaunal species in the Natural Protected Areas of Tabasco, Mexico, based on herpetofaunal surveys. Abbreviations are as follows: * = species endemic to Mexico and ** = non-native species. The numbers signifying the 14 Natural Protected Areas in Tabasco are as follows: 1 = Pantanos de Centla; 2 = Cañon del Usumacinta; 3 = Agua Blanca; 4 = La Sierra de Tabasco; 5 = Laguna del Camarón; 6 = CICN Yumká; 7 = Reserva Ecológico de la Chontalpa; 8 = Laguna de las Ilusiones; 9 = Yu-Balcah; 10 = Cascadas de Reforma; 11 = Río Playa; 12 = Grutas del Cerro Coconá; 13 = Laguna Mecoacán; and 14 = Guaritec.

Taxon	Natural Protected Area													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Xantusiidae (2 species)														
Lepidophyma flavimaculatum		+	+	+								+		
*Lepidophyma tuxtlae**														
Xenosauridae (1 species)														
Xenosaurus rackhami														
Boidae (1 species)														
Boa imperator	+		+		+	+	+	+			+		+	
Colubridae (20 species)														
Dendrophidion vinitor				+										
Drymarchon melanurus	+	+	+	+						+			+	
Drymobius margaritiferus		+	+	+		+	+	+						
Ficimia publia			+	+								+		
Lampropeltis polyzona	+													
Leptophis ahaetulla			+	+								+		
Leptophis mexicanus	+	+		+										
Masticophis mentovarius	+	+										+		
Mastigodryas melanolomus	+		+									+		
Oxybelis fulgidus														
Oxybelis potosiensis		+	+	+								+		
Phrynonax poecilonotus		+	+	+								+	+	
Pseudelaphe flavirufa				+										
Senticolis triaspis	+	+		+						+			+	
Spilotes pullatus	+			+		+	+	+				+		
Stenorrhina degenhardtii														
Stenorrhina freminvillii														
Tantilla schistosa				+										
Tantilla rubra		+												
Tantillita lintoni		+												
Dipsadidae (27 species)														
Adelphicos visoninum			+											
Amastridium sapperi				+										
Clelia scytalina				+										
Coniophanes bipunctatus	+	+		+										
Coniophanes fissidens		+		+										
Coniophanes imperialis	+	+		+								+		
Coniophanes quinquevittatus	+	+		+										
Coniophanes schmidti		+												
Conophis lineatus	+	+												
Dipsas brevifacies		+												
Geophis carinosus				+										
*Geophis laticinctus**				+					+					

Table 23 (continued). Distribution of herpetofaunal species in the Natural Protected Areas of Tabasco, Mexico, based on herpetofaunal surveys. Abbreviations are as follows: * = species endemic to Mexico and ** = non-native species. The numbers signifying the 14 Natural Protected Areas in Tabasco are as follows: 1 = Pantanos de Centla; 2 = Cañon del Usumacinta; 3 = Agua Blanca; 4 = La Sierra de Tabasco; 5 = Laguna del Camarón; 6 = CICN Yumká; 7 = Reserva Ecológico de la Chontalpa; 8 = Laguna de las Ilusiones; 9 = Yu-Balcah; 10 = Cascadas de Reforma; 11 = Río Playa; 12 = Grutas del Cerro Coconá; 13 = Laguna Mecoacán; and 14 = Guaritec.

Taxon	Natural Protected Area													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Geophis sartorii		+		+				+				+	+	
Imantodes cenchoa			+	+								+		
Imantodes gemmistratus	+			+						+		+	+	+
Leptodeira frenata		+	+	+					+			+		
Leptodeira maculata				+										
Leptodeira septentrionalis	+		+	+	+	+	+	+		+		+		
Ninia diademata		+		+								+		
Ninia sebae	+	+	+									+	+	
Oxyrhopus petolarius		+	+	+								+	+	
Pliocercus elapoides	+			+								+		
Rhadinaea decorata		+	+	+								+		
Sibon dimidiatus				+								+		
Sibon nebulatus			+	+										
Tretanorhinus nigroluteus	+		+	+		+	+	+		+	+		+	
Xenodon rabdocephalus				+					+					
Elapidae (2 species)														
*Micrurus diastema**				+							+	+		
Micrurus elegans				+										
Leptotyphlopidae (1 species)														
Epictia goudotii	+				+	+		+			+			
Natricidae (3 species)														
Nerodia rhombifera	+							+		+				
Thamnophis marcianus	+			+								+		
Thamnophis proximus	+									+			+	
Sibynophiidae (1 species)														
Scaphiodontophis annulatus		+	+	+					+			+	+	
Typhlopidae (2 species)														
Amerotyphlops tenuis		+		+				+				+		
*Indotyphlops braminus***							+	+					+	
Viperidae (7 species)														
Agkistrodon russeolus		+		+						+				
Bothriechis schlegelii			+	+						+				
Bothrops asper	+	+	+	+	+	+	+	+	+	+	+	+	+	
Crotalus tzabcan		+								+				
Metlapilcoatlus mexicanus				+										
Porthidium nasutum		+		+										
Testudines (12 species)														
Cheloniidae (2 species)														
Chelonia mydas														
Lepidochelys kempii														
Chelydridae (1 species)														

Table 23 (continued). Distribution of herpetofaunal species in the Natural Protected Areas of Tabasco, Mexico, based on herpetofaunal surveys. Abbreviations are as follows: * = species endemic to Mexico and ** = non-native species. The numbers signifying the 14 Natural Protected Areas in Tabasco are as follows: 1 = Pantanos de Centla; 2 = Cañon del Usumacinta; 3 = Agua Blanca; 4 = La Sierra de Tabasco; 5 = Laguna del Camarón; 6 = CICN Yumká; 7 = Reserva Ecológico de la Chontalpa; 8 = Laguna de las Ilusiones; 9 = Yu-Balcah; 10 = Cascadas de Reforma; 11 = Río Playa; 12 = Grutas del Cerro Coconá; 13 = Laguna Mecoacán; and 14 = Guaritec.

Taxon	Natural Protected Area													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Chelydra rossignonii	+			+							+	+		
Dermatemydidae (1 species)														
Dermatemys mawii	+	+									+			
Dermochelyidae (1 species)														
Dermochelys coriacea														
Emydidae (1 species)														
Trachemys venusta	+					+		+		+	+		+	+
Geoemydidae (1 species)														
Rhinoclemmys areolata	+										+		+	
Kinosternidae (3 species)														
Kinosternon acutum	+	+					+			+			+	
Kinosternon leucostomum	+			+		+		+			+		+	
Kinosternon scorpioides	+		+				+	+		+	+			
Staurotypidae (2 species)														
Claudius angustatus	+					+		+		+	+		+	
Staurotypus triporcatus	+				+	+		+		+	+	+		
Total	70	82	61	111	18	27	26	38	24	39	29	73	43	18

such information is available, generally it is assembled in a sufficiently detailed management plan that, in the best-case scenario, is used to justify the recognition of a given natural protected area. Oftentimes, however, the management plan is drawn up after the official designation of the protected area, or does not exist at the time of the designation. This scenario often is the case with herpetofaunal surveys.

In order to assess the extent to which the natural protected areas of Tabasco are able to protect the state herpetofauna, we collected a variety of data on these areas (Table 22). The number of these areas in Tabasco is rather substantial, amounting to 14 entities, which is the same number as seen in the state of Puebla (Woolrich-Piña et al. 2017). The Mexican Federal government administers two of these 14 areas, 11 are administered at the state level, and one is a private reserve. The 14 areas range in size from seven to 302,707 ha. Their total area is 743,808.5 ha or 7,438.1 km^2, which is 30.1% of the total area of the state and close to three times the proportion occupied by the 14 areas located in Puebla (Woolrich et al. 2017). In Tabasco, these areas were established relatively recently, during the 33-year period from 1988 to 2019. The representation of these areas among the physiographic regions of Tabasco is skewed toward the Llanura Costera de Golfo Sur or Gulf Coastal Lowlands, with 10 of the 14 located there. Three areas are found within the Sierras del Norte de Chiapas and only one in the Sierras Baja del Petén.

With respect to the range of facilities available in these 14 protected areas, eight have the full range (Table 22), and the remaining six have fewer. A major concern for the stability of the state's protected areas is that, to some degree, landowners occupy nine of the 14 (64.3%) areas. Unfortunately, the nine occupied areas include all of the largest ones, and the largest area not occupied by landowners encompasses only 572 hectares (5.72 km^2). Also unfortunate is that only five of the 14 areas have had management plans developed for them. Fewer than half (six) of the 14 areas have had herpetofaunal surveys conducted for them. Below we examine the impact of this situation on the protection of the state's herpetofauna.

Of the 165 native species known from Tabasco, all but seven (158, or 95.8%) have been recorded from one or more of the state's natural protected areas (Table 23). In addition, all five non-native species have been recorded from one or more of these areas (Table 24). The number of species recorded from these 14 areas ranges from 18 in PE Laguna del Camarón and ADVC Guaritec to 112 in PE La Sierra de Tabasco (Table 23). The seven species that are not represented in any of the 14 areas are: *Rheohyla miotympanum**; *Bolitoglossa veracrucis**; *Lepidophyma tuxtlae**; *Xenosaurus rackhami*; *Chelonia mydas*; *Lepidochelys kempii*; and *Dermochelys coriacea*.

These seven species include three country endemics, and all three of the sea turtles known from the state.

Unlike the situation commonly encountered in the other states surveyed in the MCS, a high percentage of the known herpetofauna in Tabasco has been documented in the 14 natural protected areas in the state (Table 24). To date, of the 162 species thus far recorded from these areas, most (141, or 87.0%) are non-endemic species, which is a similar percentage (85.3%) for the representation of non-endemic species in the herpetofauna as a whole (Table 9). In Tabasco, 16 of the 162 (9.9%) species known from these areas are country endemics, again similar to the percentage (11.8%) for the state as a whole (Table 9). All five of the non-native species (100%) have been shown to occur in the natural protected areas in the state, which is not desirable, as these species have been recorded in from one to all 14 of these areas. Nonetheless, the goal of complete representation of the native herpetofauna in the established natural protected areas is within reach, as only seven species need to be added. As noted above, however, four of these seven species are country endemics and three are sea turtles. All but one of these species have been recorded from only a single physiographic region (Table 4), with the four terrestrial species documented from the Sierra del Norte de Chiapas and the three marine species from the Gulf Coastal Plain. Apparently, a special effort must be undertaken to incorporate all seven species within the existing system of natural protected areas.

Conclusions and Recommendations

Conclusions

A. The herpetofauna of Tabasco presently consists of 165 native species, including 38 anurans, five salamanders, one caecilian, two crocodylians, 107 squamates, and 12 turtles. In addition, five non-native species have been recorded from the state, including one anuran and four squamates.

B. We recognize three physiographic regions in Tabasco: the Gulf Coastal Plain (GCP), the Sierras Bajas del Petén (SBP), and the Sierra Norte de Chiapas (SNC).

C. The three physiographic regions we recognize in Tabasco support from 88 species in the Gulf Coastal Plain (GCP) to 145 in the Sierra del Norte de Chiapas (SNC), with an intermediate number of 93 in the Sierra Bajas del Petén (SBP).

D. The numbers of species shared among the physiographic regions range from 61 between the GCP and the SBP to 79 between the SNC and the SBP. The Coefficient of Biogeographic Resemblance (CBR) values range from 0.61 between the GCP and the SNC to 0.67 between the GCP and the SBP. The UPGMA dendrogram (Fig. 5) indicates that the SBP and GCP cluster at the 0.67 level, while the SNC clusters to the previous pair at the 0.64 level. This pattern indicates that all three regions are closely aligned at a relatively intermediate level of overall resemblance.

E. The level of herpetofaunal endemism in Tabasco is relatively low. Of the 165 recorded native species, only 20 are country endemics (12.1%), including eight anurans, three salamanders, and nine squamates. No state endemics are known from this state.

F. The distribution status of the 170 species comprising the Tabasco herpetofauna is as follows (in decreasing order of species numbers): non-endemics (145, 85.3%); country endemics (20, 11.8%); and non-natives (5, 2.9%). Of the 145 non-endemic species, their allocation among six of the nine distributional categories are as follows: MXCA (95, 65.5%); MXSA (34, 23.4%); USCA (eight, 5.5%); USSA (four, 2.7%); OCEA (three, 2.1%); and MXUS (one, 0.7%).

G. The principal environmental threats to the herpetofauna of Tabasco are deforestation, agricultural activities, roads, soil contamination and oil extraction, myths and cultural factors (gastronomy), illegal commerce, and forest fires.

H. The conservation status of the Tabasco herpetofauna was evaluated by using the SEMARNAT, IUCN, and EVS systems. As in previous MCS entries, the SEMARNAT system was determined to be of limited value, given that of 165 native species distributed in Tabasco, only 56 (33.9%) have been assessed using this system. A comparison of the SEMARNAT and distributional categorizations demonstrates that the majority of the species in Tabasco that have not been evaluated (98, 59.4%) are non-endemic species. Otherwise, the species that have been assessed also are primarily non-endemic species (47 or 28.5%), indicating no bias toward the consideration of country endemic species.

I. The results of the application of the IUCN system (by category and proportion) are: CR (four, 2.4% of 165 native species); EN (four, 2.4%); VU (11, 6.7%); NT (10, 6.1%); LC (85, 51.5%); DD (four, 2.4%); and NE (47, 28.5%).

J. A comparison of the IUCN and distributional categorizations illustrates that most of the 165 native species (132, 80.0%) are either allocated to the LC category (85, 51.5%) or Not Evaluated (NE; 47, 28.5%).

K. The application of the EVS system of conservation assessment to the 162 native non-marine species of Tabasco demonstrates that the categorical values increase slightly from low vulnerability (66, 40.7% of 162 native non-marine species) to medium vulnerability (69, 42.6%), and then decrease markedly at high vulnerability (27, 16.7%).

L. A comparison of the IUCN and EVS conservation status categorizations demonstrates that only 16 of the 27 high vulnerability species (59.3%) are placed in the three "threat categories" (CR, EN, or VU), while 66 low vulnerability species or 77.6% are among the 85 species in the IUCN LC category. As found in previous MCS studies, these two conservation systems lacked correspondence when applied to the Tabasco herpetofauna.

M. An examination of the conservation status of the species allocated to the IUCN DD, NE, and LC categories indicates that many of these 136 species (82.4% of the 165 native species) have not been assessed adequately compared to their respective EVS values. Thus, we strongly recommend that these species be reassessed to better demonstrate their propects for future survival.

N. The Relative Herpetofaunal Priority (RHP) measure was utilized to determine the conservation significance of the three regional herpetofaunas in Tabasco. This analysis demonstrates that the herpetofauna of the Sierra del Norte de Chiapas is the most significant among the three regions, inasmuch as it supports the greatest numbers of country endemic species and high vulnerability species. The two other areas differ in their rankings (i.e., the rankings are reversed) based on these two RHP measures.

O. The number of protected areas in Tabasco is 14, of which the Mexican Federal Government administers two, while 11 are administered at the state level, and one is a private reserve. These 14 areas have been established relatively recently, from 1988 to 2019. Collectively, these areas comprise 30.1% of the total area of the state. Most of these areas (10 of the 14) are located in the Gulf Coastal Plain, while three are found in the Sierra del Norte de Chiapas, and only one is in the Sierras Baja del Petén. Landowners occupy nine (64.3%) of the 14 areas, an undesirable situation with respect to the protection of the included herpetofaunal species. Unfortunately, only five of the 14 areas have developed management plans. In addition, only six of the 14 have completed herpetofaunal surveys.

P. One highly desirable aspect, however, is that 158 (95.8%) of the 165 native species from the state have been recorded from one or more of the 14 areas. On the other hand, however, all five non-native species known from the state also are found in one or more of these areas. Of the 158 native species, 141 are non-endemics and 17 are country endemics.

Q. Future conservation efforts should be directed toward either locating sustainable populations of the seven unrecorded species within existing natural protected areas or establishing new areas, or perhaps enlarging existing areas to encompass these species. In addition, herpetofaunal surveys need to be prepared for the eight areas presently lacking them.

Recommendations

A. Our principal interest in preparing this 14th entry in the MCS is to document the composition, physiographic distribution, and conservation status of the 165 native species constituting the herpetofauna of Tabasco. The use of the EVS conservation system demonstrates that the categorical values increase only slightly from low vulnerability (66 species) to medium vulnerability (69 species), and then decrease markedly at high vulnerability (27). The Relative Herpetofaunal Priority measure indicates that the herpetofauna of the Sierra del Norte de Chiapas is the most significant among the three physiographic regions in Tabasco, because it supports the highest numbers of country endemic species and high vulnerability species.

B. The most important conservation challenge in Tabasco is to conduct the herpetofaunal surveys for eight of the 14 protected areas, with the hope that populations of the species not known to be represented within this system can be found in one or more of the areas located in the Gulf Coastal Plain and Sierra del Norte de Chiapas.

C. Once the presence of the entire native herpetofauna has been ascertained in the system of natural protected areas, then the next step will be to establish monitoring programs for all native species in order to guarantee their long-term survival. We submit that these steps need to be taken with the greatest speed, given that Tabasco is the 20th most populous state in Mexico and the 12th most densely populated.

"Living wild species are like a library of books still unread. Our heedless destruction of them is akin to burning the library without ever having read its books."

John D. Dingell (1991)

Acknowledgments.—We are grateful to the following individuals for providing their photographs for this article: Jenny del Carmen Estrada-Montiel, Coral J. Pacheco-Figueroa, José del Carmen Gerónimo-Torres, Manuel Alberto Hernández-May, Marco Antonio Torrez-Pérez, Manuel Hernández-May, and Marco Antonio López-Luna. We also are very thankful to Guillermo Woolrich-Piña for his perceptive and helpful review of the manuscript.

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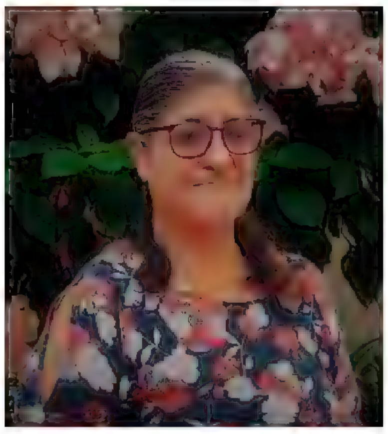
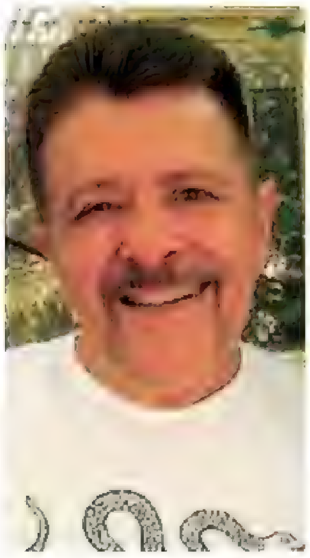


Ma. Del Rosario Barragán-Vázquez graduated with a Master's degree in Environmental Sciences from the Universidad Juárez Autónoma de Tabasco (UJAT) in Villahermosa, Tabasco, Mexico. She is a full-time Research Professor at UJAT in the Biology and Environmental Management degree programs. She is interested in the study of amphibians and reptiles at the community level, and from ecological, taxonomic, and management and utilization points of view. She has undertaken academic appointments at CINVESTAV-Mérida, Faculty of Sciences, UNAM, and at the Universidad Veracruzana, with work on amphibian cultivation, taxonomy, and behavior. She has participated in research projects on the herpetofauna in the municipalities of the Sierra de Tabasco, and has authored or co-authored various articles, notes, and book chapters, primarily on the community level biodiversity and population genetics in turtles. She is in charge of the Colección de Anfibios y Reptiles de Tabasco (CART), curated within the División Académica de Ciencias Biológicas de la UJAT.

Liliana Ríos-Rodas has a degree in Biology from the Universidad Juárez Autónoma de Tabasco (UJAT), a Master's degree in Agricultural Sciences and Natural Resources from the Universidad Autónoma de México, and a Ph.D. in Ecology and Management of Tropical Systems from UJAT. Her main research topics involve the ecology of communities and populations of amphibians and reptiles of Tabasco, focusing on riparian ecosystems of tropical environments. She has worked on the ecomorphology of the genus *Sceloporus*, geometric morphometry in *Dryophytes plicatus*, and trophic ecology in *Craugastor berkenbuschii*. Liliana has participated in genetic conservation projects for *Dermatemys mawii* and *Trachemys venusta,* and in updating the Tabasco Amphibian and Reptile Collection (CART). She is the author or co-author of several articles on the distribution, diversity, and conservation of the herpetofauna of Tabasco.

Lydia Allison Fucsko, who resides in Melbourne, Australia, is an environmental activist and amphibian conservationist. As a photographer with international publications, she has taken countless amphibian photographs, including photo galleries of frogs mostly from southeastern Australia. Dr. Fucsko has a Bachelor of Humanities from La Trobe University (Bundoora, Victoria, Australia) and a Diploma in Education from the University of Melbourne (Parkville, Victoria, Australia). She has postgraduate diplomas in computer education and in vocational education and training from the University of Melbourne (Parkville). Additionally, Dr. Fucsko has a Master's degree in Counseling from Monash University (Clayton, Victoria, Australia). She received her Ph.D. in Environmental Education, which promoted habitat conservation, species perpetuation, and global sustainable management, from Swinburne University of Technology (Hawthorn, Victoria, Australia), while being mentored by the late Australian herpetologist and scholar Dr. Michael James Tyler (Order of Australia recipient). As a sought-after educational consultant, Dr. Fucsko has academic interests that include: clinical psychology, focusing on psychopathology; neuroscience and empathy; environmental education for sustainable development; sentient ecology; academic writing; and creative writing, which includes poetry and creative non-fiction books for children and young adults. Dr. Fucsko also is the senior author (with Boria Sax) of a chapter in the 2019 *Springer Encyclopedia of Sustainability in Higher Education* entitled "Learning activities for environmental education for sustainable development." Recently, Dr. Fucsko has co-authored an obituary of Jaime D. Villa, a study of the introduced Mesoamerican herpetofauna, a treatment of the conservation prospects of the Mesoamerican salamander fauna, papers on the herpetofauna of Veracruz and Querétaro, Mexico, a review of the book *Advances in Coralsnake Biology*, and a study on the biological and cultural diversity of Oaxaca, Mexico, among several other academic papers. In 2020, the species *Tantilla lydia*, with the suggested common name of Lydia's Little Snake, was named in her honor.

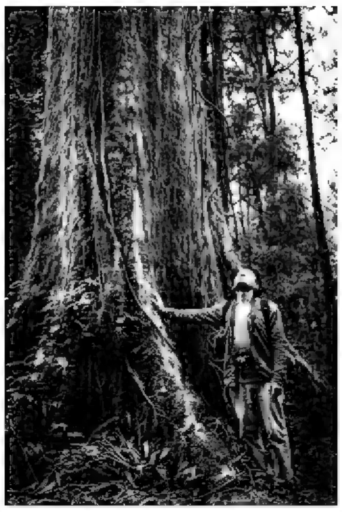


Louis W. Porras graduated in 1971 with a degree in Biology from what today is known as Miami-Dade College in Miami, Florida, USA. Over his career he has authored or co-authored over 60 academic publications, including the descriptions of two new species, and two taxa have been named in his honor. Louis developed an interest in herpetology at an early age in his native Costa Rica. His passion for the field led him to travel to many remote areas, including throughout the Bahamas, the United States, Mesoamerica, and parts of South America. In 1968, he worked at the Houston Zoological Gardens, and from 1982 to 1984 at Utah's Hogle Zoo. In 1976, he attended the inaugural meeting of the International Herpetological Symposium (IHS), and later served the group as Vice-President and President. In 1993, along with Gordon W. Schuett, he helped launch the journal *Herpetological Natural History*, and for IHS' 20th anniversary, in recognition of his contributions, three former Presidents dedicated the book *Advances in Herpetoculture* in his honor. Louis' career in publishing began in 1995, when as a member of Canyonlands Publishing Group he helped publish *Fauna* magazine. In 2002 he founded Eagle Mountain Publishing, LC, which has published such herpetological titles as *Biology of the Vipers* (2002), *Biology of the Boas and Pythons* (2007)*, Amphibians, Reptiles, and Turtles in Kansas* (2010), *Conservation of Mesoamerican Amphibians and Reptiles* (2010), and *Amphibians and Reptiles of San Luis Potosí* (2013). From 2014 to 2018 he was the Publisher and Managing Editor of the journal *Mesoamerican Herpetology*, and recently he was the Publisher and Co-editor of the book *Advances in Coralsnake Biology*: *with an Emphasis on South America.*

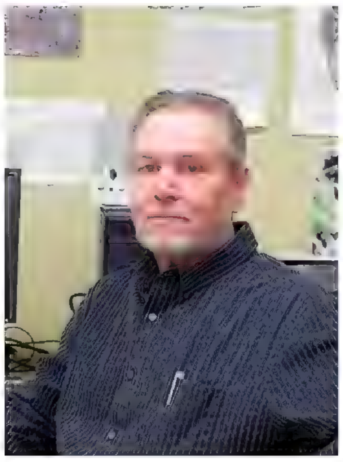
Vicente Mata-Silva is a herpetologist originally from Río Grande, Oaxaca, Mexico. His interests include ecology, conservation, natural history, and biogeography of the herpetofaunas of Mexico, Central America, and the southwestern United States. He received a B.S. degree from the Universidad Nacional Autónoma de México (UNAM), and M.S. and Ph.D. degrees from the University of Texas at El Paso (UTEP). Vicente is an Assistant Professor of Biological Sciences at UTEP, in the Ecology and Evolutionary Biology Program, and Co-Director of UTEP's Indio Mountains Research Station, located in the Chihuahuan Desert of Trans-Pecos, Texas, USA. To date, Vicente has authored or co-authored over 100 peer-reviewed scientific publications. He also was the Distribution Notes Section Editor for the journal *Mesoamerican Herpetology*, and is currently Associate Editor for the journal *Herpetological Review*.

Arturo Rocha is a Ph.D. student in the Ecology and Evolutionary Biology program at the University of Texas at El Paso. His interests include the study of the biogeography, physiology, and ecology of amphibians and reptiles in the southwestern United States and Mexico. A graduate of the University of Texas at El Paso, his thesis centered on the spatial ecology of the Trans-Pecos Rat Snake (*Bogertophis subocularis*) in the northern Chihuahuan Desert. To date, he has authored or co-authored over 20 peer-reviewed scientific publications.

Dominic L. DeSantis is an Assistant Professor of Biology at Georgia College and State University, Milledgeville, Georgia, USA, in the Department of Biological and Environmental Sciences. Dominic's research interests broadly include the behavioral ecology, conservation biology, and natural history of herpetofauna. In addition to ongoing collaborative projects associated with the Mesoamerican Research Group, much of Dominic's current research focuses on using novel animal-borne sensor technologies to study the behavior of snakes in the field. While completing his Ph.D. at the University of Texas at El Paso, Dominic accompanied Vicente Mata-Silva, Elí García-Padilla, and Larry David Wilson on survey and collecting expeditions to Oaxaca in 2015, 2016, and 2017, and is a co-author on numerous natural history publications produced from those visits, including an invited book chapter on the conservation outlook for herpetofauna in the Sierra Madre del Sur of Oaxaca.



Elí García-Padilla is a Social Biologist and Professional Photographer with more than 12 years of experience in the formal study and photo documentation of the biological and cultural diversity of Mexico. He has published one book, entitled *Mexican Biodiversity: the Snake, the Jaguar and the Quetzal,* and more than 100 formal contributions on knowledge, the communication of science and the conservation of Mesoamerican biodiversity. Since 2006, he has been exploring Oaxaca and Chiapas, which are the most biodiverse and multicultural states in Mexico. In 2017, he began to enter the mythical region of Los Chimalapas in the Isthmus of Tehuantepec, which is the most biologically rich region in all of Mexico, under a community social conservation scheme. Elí has published his photographic work in prestigious magazines such as *National Geographic* in Spanish and *Cuartoscuro*. In 2020, he co-founded the *Mesoamerican Biodiversity* initiative with the aim of creating a community around the dissemination of the most important wealth of Mexico, which is its biodiversity and its culture. His writings are published regularly in *Oaxaca Media*, the *Jornada Ecológica* and the *Ojarasca Supplement* of *La Jornada*.



Jerry D. Johnson is Professor of Biological Sciences at The University of Texas at El Paso, and has extensive experience studying the herpetofauna of Mesoamerica, especially that of southern Mexico. Jerry is the Director of the 40,000-acre Indio Mountains Research Station, and was a co-editor on the book *Conservation of Mesoamerican Amphibians and Reptiles* and co-author of four of its chapters. He was also the senior author of the recent paper "A conservation reassessment of the Central American herpetofauna based on the EVS measure" and is Mesoamerica/Caribbean editor for the Geographic Distribution section of *Herpetological Review*. Jerry has authored or co-authored over 130 peer-reviewed papers, including two 2010 articles, "Geographic distribution and conservation of the herpetofauna of southeastern Mexico" and "Distributional patterns of the herpetofauna of Mesoamerica, a Biodiversity Hotspot." One species, *Tantilla johnsoni*, has been named in his honor. Presently, he is an Associate Editor and Co-chair of the Taxonomic Board for the journal *Mesoamerican Herpetology*.

Larry David Wilson is a herpetologist with lengthy experience in Mesoamerica. He was born in Taylorville, Illinois, USA, and received his university education at the University of Illinois at Champaign-Urbana (B.S. degree) and at Louisiana State University in Baton Rouge (M.S. and Ph.D. degrees). He has authored or co-authored more than 460 peer-reviewed papers and books on herpetology. Larry was the senior editor of *Conservation of Mesoamerican Amphibians and Reptiles* and a co-author of seven of its chapters. His other books include *The Snakes of Honduras*, *Middle American Herpetology*, *The Amphibians of Honduras*, *Amphibians & Reptiles of the Bay Islands and Cayos Cochinos, Honduras*, *The Amphibians and Reptiles of the Honduran Mosquitia*, and *Guide to the Amphibians & Reptiles of Cusuco National Park, Honduras*. To date, he has authored or co-authored the descriptions of 75 currently-recognized herpetofaunal species, and seven species have been named in his honor, including the anuran *Craugastor lauraster*, the lizard *Norops wilsoni*, and the snakes *Oxybelis wilsoni*, *Myriopholis wilsoni*, and *Cerrophidion wilsoni*. In 2005, he was designated a Distinguished Scholar in the Field of Herpetology at the Kendall Campus of Miami-Dade College in Miami, Florida, USA. Currently, Larry is a Co-chair of the Taxonomic Board for the website *Mesoamerican Herpetology*.

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Amphibian & Reptile Conservation
16(2) [General Section]: 62–68 (e316).

Reproductive characteristics of the Burmese Narrow-headed Softshell Turtle, *Chitra vandijki*, in captivity

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***Abstract.*—The purpose of this study was to provide basic data for the breeding biology of *Chitra vandijki* and to contribute to the conservation of this species. The Burmese Narrow-headed Softshell Turtle, *Chitra vandijki*, is a CITES Appendix I-listed species, and biological information on wild and captive *C. vandijki* is relatively scarce. In 2019, we studied the reproductive biology of two *C. vandijki* specimens (a female and a male) that had been in captivity for approximately 25 years. The oviposition period of the domesticated female *C. vandijki* was from June to August. The female laid eggs at night, and no egg protection behavior was observed. The female *C. vandijki* laid five clutches of eggs in a year representing 564 eggs in total, with 100–131 eggs/clutch, and the interval between successive clutches was 9–28 d. The fertilization rate of *C. vandijki* was 90.4%, and the hatching rate was 38.6%. The eggs were spherical and rigid, with an average mass of 15.04 ± 0.65 g and an average diameter of 2.96 ± 0.22 cm. The average hatching period of *C. vandijki* was 65.3 d at 28.0–29.0 °C, and the average accumulated incubation temperature was 44,688.6 °C-h. The average mass of newly hatched neonates was 10.51 ± 0.57 g, and the average mass of juvenile *C. vandijki* reached 150.37 ± 53.86 g after one year of feeding live fry in a greenhouse.**

Keywords. Burmese Narrow-headed Softshell Turtle; captive-breeding; *Chitra vandijki*; conservation; egg laying; juvenile; threatened species

Citation: Hong X, Zhu X, Chen C, Cai X, Li Y, Li X. 2022. Reproductive characteristics of the Burmese Narrow-headed Softshell Turtle, *Chitra vandijki*, in captivity. *Amphibian & Reptile Conservation* 16(2) [General Section]: 62–68 (e316).

Accepted: 22 February 2022; **Published:** 1 September 2022

Introduction

The Burmese Narrow-headed Softshell Turtle, *Chitra vandijki*, is a large turtle with a straight-line carapace length of up to 1 m. It is listed on CITES Appendix I and classified as Critically Endangered (CR) on the *IUCN Red List of Threatened Species* (Rhodin et al. 2018; Platt et al. 2021). It is mainly distributed in rivers in Myanmar and Thailand (Platt et al. 2014). The abundance and distribution of *C. vandijki* have been sharply reduced because of human hunting and habitat destruction (Kuchling et al. 2004; Platt et al. 2005, 2014). Because little is known about the turtle's ecological habits, successful cases of artificial breeding are very few and knowledge of its breeding biology is extremely lacking (Platt et al. 2018, 2020).

Because the external appearance of *C. vandijki* is similar to the Asian Giant Softshell Turtle, *Pelochelys cantorii*, and given the demands of the Chinese wild animal market, *C. vandijki* has been illegally traded to China as food or for rearing in the last century. Although *P. cantorii* in China is Critically Endangered (Gong et al. 2017; Hong et al. 2019; Wu et al. 2020), we have successfully carried out artificial breeding of six *P. cantorii* (three females and three males) turtles since 2014 (Zhu et al. 2015; Hong 2020). At present, we have bred more than 800 *P. cantorii* between 1 and 6 years old (Ministry of Agriculture and Rural Affairs of People's Republic China 2020). Based on our successful experience in the artificial breeding of captive *P. cantorii*, we carried out research on the reproductive biology of two captive *C. vandijki*, and the mitochondrial genomes of the individual hatched offspring confirmed their identity as Burmese Small-headed Turtles (Chen et al. 2021). The findings of this study enrich the basic biological data of *C. vandijki* and provide a theoretical basis for its conservation biology.

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Materials and Methods

Captive Care, Conditions, and Management

Two *C. vandijki*, one male and one female, were accidentally captured and rescued from the waters of the Mekong River at the border between Myanmar, Laos, and Guanli Town, Mengla County, Xishuangbanna Prefecture, Yunnan Province, China in 1995. Their body weights at the time of capture were approximately 3 kg and 7 kg, respectively.

The two *C. vandijki* were raised in an outdoor fish pond at an elevation of 570 m asl (21°35'40.84"N 101°14'5.02"E) in Xishuangbanna Prefecture, Yunnan Province, China. This region has a north tropical and south tropical humid monsoon climate, which includes a long summer without winter. The annual average temperature is between 18.6 and 21.9 °C, and the annual average precipitation is between 1,200 and 1,700 mm. The dimensions of the pond were 30 m × 25 m, the water depth was 1.2 m, and the bottom mud was 30–40 cm thick (Fig. 1A). In 2012, a 25 m × 2 m nesting sand pond with a depth of 60 cm was built on the side of the main pond, and there was a shed above the sand pool for shade. Tiles were used to build an incline of about 30° so the turtles could climb up from the water to the sand pond (Fig. 1A–B). In the pond, Tilapia *Oreochromis niloticus*, Carp *Cyprinus carpio*, and Crucian Carp *Carassius auratus* were cultured together, and the *C. vandijki* lived by feeding on these fish.

In December 2018, the fish pound was cleared, and the large fish were removed. From February to May 2019, 200 kg of live fish fry, including Carp, Crucian Carp, and Mud Carp (*Cirrhinus molitorella*) with body lengths of 3–5 cm, were regularly added to the pond to serve as the food for improving the cultivation of *C. vandijki*.

Collection and Hatching of Eggs

In April 2019, the stones and plants in the spawning sand pool were cleared, and the sand was raked loose and sieved. From May to July, water was sprayed irregularly into the spawning sand pond to ensure that the sand remained damp. A surveillance camera was installed above the spawning pool to observe the oviposition activity of *C. vandijki*. For the first clutch, the eggs were incubated *in situ* for 25 days, the clutch was dug manually, and artificial incubation was continued. For the other clutches, within 16–24 h after the turtle had laid the eggs, they were collected by excavating the nest. The numbers of eggs and fertilized eggs were counted and recorded. The diameter of each egg was measured with a Vernier caliper (± 0.01 cm), and the egg weight was measured using an electronic balance (± 0.01 g).

The incubators for fertilized eggs were plastic boxes with dimensions of 57 × 41 × 36 cm. The medium was sieved fine river sand, and the moisture content of the sand was 8–10% (weight ratio, Fig. 1C). The thickness of the sand pile was approximately 15 cm. The fertilized eggs in a given clutch were arranged on the sand pile in

Fig. 1. Artificial rearing facility of Burmese Narrow-headed Softshell Turtles: **(A)** breeding pond, **(B)** nesting area, **(C)** incubation box, **(D)** rearing facilities.

the incubator and covered with 2 cm of fine sand with the same dampness. The incubator was then covered. The temperature of the incubator was controlled by an indoor air conditioner, and maintained at 28.0–29.0 °C. Water was sprayed regularly onto the sand to control the humidity.

Cultivation of Hatchlings

After emergence, the hatchlings were observed and photographed. The body mass of each hatchling was obtained using an electronic balance (± 0.01 g). The length and width of the carapace and the length and width of the snout of each juvenile were measured using a caliper (± 0.01 cm). Hatchlings were reared according to the rearing method of Asian Giant Softshell Turtle (*P. cantorii*) hatchlings (Hong et al. 2018), and cultured in six custom-designed round buckets with a diameter of 1.2 m and a water depth of 0.5 m. The cultivation density was 25–30 individuals/m^2, the bottom of the bucket contained 15 cm of fine sand, and the water was filtered through circulation (Fig. 1D). The pH of the water was measured regularly and adjusted to 7.0–7.5 with quicklime. The neonates were fed live Mosquito Fish, *Gambusia affinis*. The temperature was controlled by air conditioning and the water temperature was maintained at 26.0–31.0 °C. In July 2020, five juvenile *C. vandijki* were randomly selected from each barrel. The body mass and length and width of the carapace of 30 hatchlings were measured.

Statistics

The data shown below and labeled as "this study" are expressed as the mean ± SD, and were compared and analyzed using ANOVA. Statistical analysis was conducted using IBM SPSS 23.0 software. All statistical tests were two-tailed, and the significance level was set as $P<0.05$.

Results and Discussion

Morphology of the Parents

In 2012, the body mass of the female *C. vandijki* was 38.0 kg. On 6 December 2018, the body masses of the female and male parental *C. vandijki* were 59.2 kg and 40.0 kg, respectively.

There were irregular, slightly fuzzy yellow stripes on the adult carapace (Fig. 2A). The longitudinal stripes on the neck and back merged behind the head, and the neck stripes were more obvious than the stripes on the back (Fig. 2B). The neck was not obviously separated from the anterior edge of the carapace. The neck of the

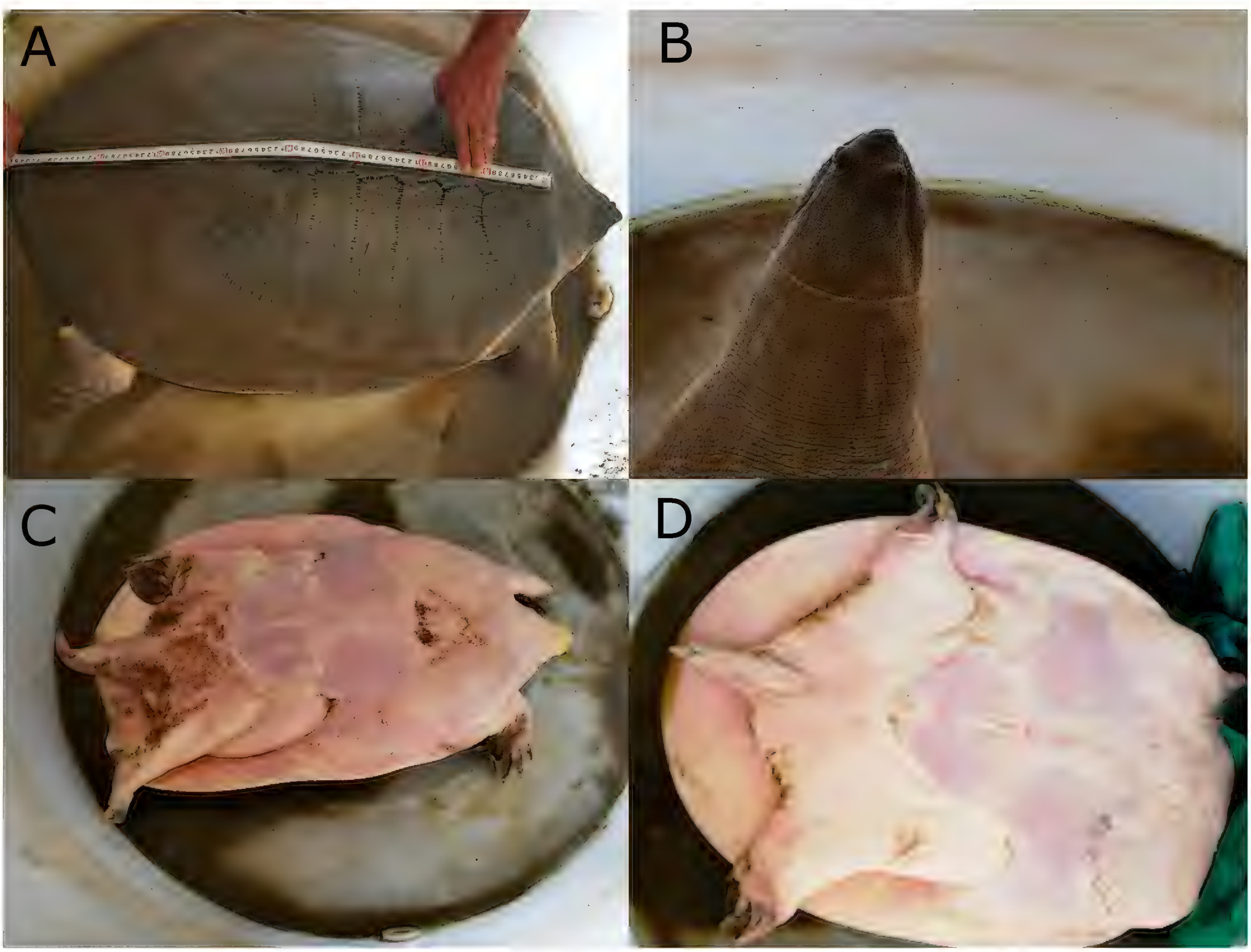

Fig. 2. Characteristics of Burmese Narrow-headed Softshell Turtles: **(A)** back; **(B)** head and neck, close-up; **(C)** male, ventral view; **(D)** female, ventral view.

Table 1. Egg laying and hatching data of Burmese Narrow-headed Softshell Turtles in 2019.

Date of egg laying	Clutch size	Number of fertilized eggs/ clutch	Fertilization rate (%)	Number of hatchings/ clutch	Hatching rate (%)
3 June 2019	101	69	69.3	43	62.3
1 July 2019	131	117	85.4	80	80.0
18 July 2019	110	105	95.5	54	68.4
27 July 2019	122	120	98.4	20	9.1
9 August 2019	100	99	99.0		
Total	564	510	90.4	197	38.6

adult *C. vandijki* was slightly short and could not turn to the middle or rear of the carapace. The front edge of the carapace was flat, without folds or warts. The head of the adult *C. vandijki* was small, and the snout was short (Fig. 2A–B).

The main morphological difference between the males and females was the tail. The tail of male *C. vandijki* was thick and long, extending out from the edge of carapace, while the tail of female *C. vandijki* was thin and short, extending no longer than the edge of the carapace (Fig. 2C–D).

Egg Laying

In 2004 and 2006, 10 and 20 eggs were laid, respectively, in the culture pond water of the parent *C. vandijki*. After the construction of the spawning sand pond, 98 *C. vandijki* hatchlings were collected from the fish pond in September 2018. However, they all died within 30 d of captive feeding following the cultivation method of the Chinese Softshell Turtle *Pelodiscus sinensis* (Zhao et al. 1997).

Beginning in June 2019, the female turtle was observed climbing up the sand dunes at night, looking for nesting sites. On the nights of 3 June to 9 August, the female turtle laid five clutches of eggs, for a total of 564 eggs. The four intervals between the five clutches were 28 d, 17 d, 9 d, and 13 d, respectively (Table 1), and the average interval was 16.75 ± 8.18 d.

The *C. vandijki* eggs were nearly round and rigid, and the calcareous layer of the eggshell was thin. The number of eggs in each clutch varied from 100 to 131 (Table 1), with an average of 112.8 ± 13.5 eggs/clutch. We randomly selected 40 eggs from the first clutch and another 40 eggs from the second clutch for measurements. The egg masses were 13.37–16.47 g (15.04 ± 0.65 g) and egg diameters were 2.76–3.15 cm (2.96 ± 0.22 cm). According to the average egg weight, the total weight of the five clutches of eggs could be estimated as 8,482.56 g, accounting for 14.335% of the maternal body weight.

Hatching and Characteristics of Hatchlings

The five clutches included 510 fertilized eggs, and the fertilization rate was 90.4%. In total, 197 hatchlings emerged, for a hatching rate of 38.6% (Table 1).

The average incubation period of the fertilized eggs was 65.3 ± 5.4 d, and the average accumulated incubation temperature was 44,688.6 °C-h at a room temperature of 28.0–29.0 °C (28.51 °C on average) based on the hatching data of the second clutch. Under artificial conditions, the hatching rate for the last four clutches of eggs was 34.9%.

The carapace of the newly hatched neonate *C. vandijki* was approximately round, with obvious yellow stripes on the neonate's back, neck, and limbs. The carapace was covered with small protuberances and the posterior edge was yellow without stripes (Fig. 3). The newly hatched neonate *C. vandijki* weighed 9.44–11.75 g (10.51 ± 0.57 g, $n = 60$, 30 neonates in the first clutch and another 30 neonates in the second clutch). The length of the neonate *C. vandijki* carapace was 4.18–4.70 cm (4.41 ± 0.13 cm), and the width of the carapace was 3.75–4.24 cm (4.01 ± 0.10 cm). The length of the snout of neonate *C. vandijki* was 0.14–0.22 cm (0.16 ± 0.02 cm) and the width of the snout was 0.15–0.24 cm (0.19 ± 0.02 cm).

The reproductive biology data for four species of softshell turtles bred in captivity are shown in Table 2. *C. vandijki*, *P. cantorii,* and the Siamese Narrow-headed Softshell Turtle (*Chitra chitra*) are all large Trionychidae

Table 2. Comparison of the reproductive biology of four species of softshell turtles in captivity.

	Burmese Narrow-headed Softshell Turtle (this study)	Siamese Narrow-headed Softshell Turtle (Kitimasak et al. 2003)	Asian Giant Softshell Turtle (Hong et al. 2018; Hong 2020)	Chinese Softshell Turtle (Yang et al. 1999; Zhou 2004)
Parent sample size (♀, ♂)	1, 1	2, 4	2, 2	>800, >100
Number of clutches/year	5	3–4	4–6	5–7
Clutch size	100–133	40–88	32–55	8–25
Egg diameter (cm)	2.96 ± 0.22	3.32 ± 0.15	3.10 ± 0.18	2.00–2.40
Egg mass (g)	15.04 ± 0.65	19.00 ± 1.67	16.82 ± 1.99	3.55–6.77
Mass of neonate (g)	10.51 ± 0.57	13.10 ± 1.03	13.60 ± 0.85	2.33–4.83
Accumulated incubation temperature (°C-h)	44,688.60	Not reported	44,886.50	36,000

Fig. 3. Hatchling of Burmese Narrow-headed Softshell Turtle.

animals with similar breeding biology, but they are very different from the Chinese Softshell Turtle, *Pelodiscus sinensis*. There are very limited breeding data for wild *C. vandijki*. Platt et al. (2020) reported that the numbers of eggs in four collected clutches were 58, 76, 89, and 102; and the diameter of the eggs was 2.01–3.66 cm (2.60–2.95 cm on average). The length of the carapace of the hatchlings was 2.73–4.10 cm (3.52 ± 0.35 cm), and the width of the carapace was 2.75–3.86 cm (3.39 ± 0.26 cm). However, data for the parent *C. vandijki* were not reported in that study. In general, in our study, the clutch size, diameter of eggs, and body size of neonate *C. vandijki* were all higher than those reported by Platt et al. (2020), suggesting that the maternal size in our study might be larger and/or that the nutritional status of *C. vandijki* in captivity is better than that in the field (Gibbons et al. 1990; Litzgus et al. 2008; Hong et al. 2018).

Based on the egg laying and hatching data, we found that the number of eggs in each clutch was relatively constant and the fertilization rate remained at a high level. However, the hatching rates of the last two clutches were relatively low (Table 1). The total mass of the five clutches of eggs accounted for approximately 14% of the body mass of the female *C. vandijki*. We considered that the low hatching rate of the last two clutches may be due to the influence of oviposition frequency and the availability of reproductive resources for the female *C. vandijki* (Jackson and Prange 1979; Ferguson et al. 1982). We speculate that too much of the energy of the female *C. vandijki* had been consumed by the late stage of oviposition, and the spawning intervals between the last two clutches were short (9 d and 13 d), which may have resulted in an insufficient energy supply for the development of the eggs, leading to improper development of the embryos. This phenomenon has been reported for *P. cantorii* (Hong et al. 2018).

Growth of Juveniles

By July 2020, 180 juvenile *C. vandijki* survived, for a survival rate of 91.4%. The body weight of juvenile *C. vandijki* was 49.80–311.10 g (150.37 ± 53.86 g, $n = 30$), the length of the juvenile carapace was 7.54–13.19 cm (11.05 ± 1.66 cm), the width of the carapace was 7.56–12.87 cm (10.84 ± 1.53 cm), the length of the juvenile snout was 0.22–0.40 cm (0.29 ± 0.05 cm), and the width of the snout was 0.23–0.43 cm (0.31 ± 0.06 cm). The living habits of *P. cantorii* and *C. vandijki* are similar; thus, the juvenile breeding method of *P. cantorii* is also suitable for *C. vandijki* and is ideal in terms of survival rate and growth rate.

P. cantorii is endangered due to overhunting and habitat destruction, and China has increased its artificial conservation efforts to gradually restore wild resources, which has achieved initial results (Ministry of Agriculture and Rural Affairs of People's Republic China 2020). Currently, the *C. vandijki* population has been greatly reduced, and so it is also in a critical condition state. For this reason, referring to the Chinese protection strategy for *P. cantorii*, we can use the limited captive population of *C. vandijki* to carry out conservation biological research in order to achieve the artificial conservation of this species, and subsequently release the captive turtles into the wild to restore the wild population.

Acknowledgments.—Thanks are due to the staff of Xishuangbanna Dai Autonomous Prefecture Fishery Technology Extension Station for the breeding turtles for more than 25 years. We also thank all those who have contributed to the conservation of *Pelochelys cantorii* and *Chitra vandijki*. The financial support for this work was provided by the Foshan City Financial Special Fund-2020, the Guangdong Agricultural Science and Technology Demonstration City Project, and the Central Public-interest Scientific Institution Basal Research Fund, CAFS (#2019ZD04, #2020TD35 and #2020ZJTD01).

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Li Xinping is a farmer who cultivates aquatic seedlings, with a special interest in the protection and breeding of turtles. Mr. Li has been rearing the two captive *Chitra vandijki* specimens used in this study for more than 25 years.

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Amphibian & Reptile Conservation
16(2) [General Section]: 69–87 (e317).

Applying population genetics to define the units for conservation management in the European Tree Frog, *Hyla arborea*

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***Abstract.*—Population genetic analyses are a powerful tool for obtaining information about cryptic genetic lineages, population structure, and the distribution of intra- and interpopulation genetic diversity across the landscape. This knowledge is crucial for establishing units for the conservation management of endangered species. Species with limited dispersal capacities, such as amphibians, are particularly affected by habitat fragmentation and reductions in gene flow among isolated populations. The European Tree Frog, *Hyla arborea*, has suffered from dramatic population declines in the last decades and is categorized as Vulnerable to Critically Endangered in its north-western distribution range. In Lower Saxony (Germany), the current distribution of the tree frog is fragmented. In this study, we aimed to assess the population structure, genetic diversity, gene flow, and migration rates in order to define the units for conservation management. Across a distribution area of 250 km², frogs were sampled at 14 localities and genotyped at seven microsatellite loci, and the *mt*DNA cytochrome *b* gene was sequenced for a subsample. Whereas microsatellite pairwise D_{est} and F_{ST} values showed genetic differentiation among nearly all sampled populations, Bayesian analyses assigned the 14 localities to two distinct genetic clusters including seven subclusters. Together with a slight correlation between geographic and genetic distance, the population structure indicates ongoing fragmentation. The cytochrome *b* haplotype distribution does not indicate divergence into *mt*lineages, but highlights the former connection of populations along the river Elbe. The results of this study suggest that the intense anthropogenic pressures in this area over the last decades have had negative genetic consequences for this species. The fragmented population structure calls for reconnection of the isolated occurrences by the implementation of conservation measures.**

Keywords. Amphibian, Bayesian assignment, conservation genetics, genetic diversity, population fragmentation, population structure

Citation: Krug A, Auffarth J, Pröhl H. 2022. Applying population genetics to define the units for conservation management in the European Tree Frog, *Hyla arborea*. *Amphibian & Reptile Conservation* 16(2) [General Section]: 69–87 (e317).

Accepted: 14 September 2022; **Published:** 24 October 2022

Introduction

Genetic diversity and connectivity mediated by migrating individuals between populations are critical for the maintenance of many threatened species and can be evaluated by population and landscape genetic analyses (Shaffer et al. 2015). Loss of connectivity disrupts gene flow between formerly connected habitats and leads to the isolation of populations. Isolation in turn imposes a more rapid erosion of genetic diversity, exacerbating the effects of genetic drift and inbreeding on local gene pools (Andersen et al. 2004; Crnokrak and Roff 1999; Hedrick and Kalinowski 2000; Luquet et al. 2011).

When reconnection of the habitats of endangered species is necessary, it is essential to determine the genetic structures and migration patterns for effective conservation management. This information can be used to delineate conservation units (e.g., Palsbøll et al. 2007), even though the concepts that are applied to define them are somewhat uneven among studies and taxa (Shaffer et al. 2015). While Evolutionary Significant Units (ESUs) are used to delineate entities which possess a long (evolutionary) history (Crandall et al. 2000; Moritz 1994), management efforts are often restricted to a more recent and regional space. In such cases, population boundaries need to be identified among which gene flow is limited. To achieve this, both mitochondrial

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and nuclear markers are informative. Mitochondrial DNA has been widely used to analyze the phylogenetic relationships of amphibian populations (Dufresnes et al. 2013; Stöck et al. 2012), while nuclear markers like microsatellites are well suited for detecting fine-scale structuring of populations and recent loss of genetic variation (Selkoe and Toonen 2006). Population genetic approaches such as Bayesian assignment tests use population allele frequencies to group individuals into genetic clusters. Together with information on genetic divergence between genetic clusters, this approach can be used to denote conservation units (Olsen et al. 2014; Rowe and Beebee 2007).

In Europe, habitat loss, fragmentation, and degradation – mostly due to anthropogenic pressure (Cushman 2006; Pimm and Raven 2000) – are the most significant threats to endangered wildlife populations (Fahrig and Merriam 1994; Sih et al. 2000; Stuart et al. 2004). Amphibian populations are especially vulnerable to fragmentation and loss of genetic variation due to their low dispersal capabilities (as reviewed in Smith and Green 2006). For safeguarding vulnerable species of this most endangered vertebrate group (Stuart et al. 2004), it is necessary to counteract genetic depletion by maintaining the exchange of individuals among populations.

The European Tree Frog has shown long-term decline in much of its Western European distribution, mainly caused by habitat fragmentation (Andersen et al. 2004; Dubey et al. 2009; Krug and Pröhl 2013). The highest genetic diversity of this species has accumulated in South-eastern Europe, where it survived in refugia during glaciations. After late-Pleistocene diversification on the Balkan Peninsula, one of several major genetic groups recolonized North and Western Europe. Postglacial expansions resulted in decreasing genetic diversity across the range and therefore increased the vulnerability of populations towards North-Western Europe (Dufresnes et al. 2013; Stöck et al. 2012). Indeed, the tree frog is not categorized as threatened in South-Eastern Europe, while it is reported to have declined and is now classified as Vulnerable to Critically Endangered in different areas in the north-west (see review in Dufresnes et al. 2013, Table S1). In Lower Saxony in Germany, where the current distribution is patchy with some main occurrences in the lowlands (Fig. 1), the conservation status of the tree frog is Endangered (see the Red List at http://www.amphibienschutz.de). Although the species was widespread in the past, severe declines have been observed mainly in the second half of the last century (Manzke and Podloucky 1995). In some places, measures for conservation management have been successful (Brandt and Lüers 2017; Buschmann et al. 2006; Richter and Mügge 2012).

For supporting further conservation activities, analyses of the genetic structure are required for assessing the genetic clusters as a way to delineate the units for conservation management (Rowe and Beebee 2007). So far, several studies have measured the genetic structure and diversity in more or less fragmented metapopulation systems (Andersen et al. 2004; Angelone and Holderegger 2009; Arens et al. 2006; Dubey et al. 2009; Edenhamn et al. 2000; Krug and Pröhl 2013). The aim of this study was to perform a conservation genetic survey of the European Tree Frog across its distribution in Lower Saxony and adjacent areas. The specific intention was to assess significant genetic differentiation in order to define those conservation units among which dispersal is restricted. The obtained information was then used to identify population management goals and to provide specific recommendations about conservation priorities to ensure the long-term survival of the tree frog in this region.

In this study, we tested hypotheses regarding population genetic structure, differentiation, and diversity in the Endangered European Tree Frog by analyzing mitochondrial sequence and nuclear microsatellite data with a series of statistical techniques. First, we tested for the existence of diverged genetic lineages. We further predicted that past population expansion and recent habitat fragmentation 1) reduced the migration among localities; 2) reduced genetic diversity as well as genetic population size within localities; and 3) resulted in significant genetic structure among the remaining tree frog localities. Therefore, 4) we expected a small to moderate effect of geographic distance on genetic differentiation as a result of the ongoing population disconnection. This work reveals ongoing population fragmentation with moderate genetic diversity for the populations of the European Tree Frog in Lower Saxony.

Materials and Methods

Sample Collection and Preparation

Fourteen sites were sampled across the tree frog distribution in Lower Saxony and adjacent distributions in North Rhine Westphalia and Saxony-Anhalt, all in Germany. We chose one sample site within each main occurrence of the tree frog in this region (Fig. 1). In the occurrence near Hannover, however, we sampled four sites: two in the west of Hannover (KZ, KO, see Table 1 for site definitions) and two in the east of Hannover (KH, BH) for a comparison of smaller scaled spatial distances. In total, 237 individuals were sampled with 5–22 individuals per sample site (Table 1). Genetic material was collected from the tips of tadpole tails and buccal swabs of adult frogs. The adults were collected from the choruses during the breeding seasons in spring 2007 and 2008. Tadpoles were sampled in summer 2007 at three localities. In this year, the climatic conditions for breeding where unfavorable and adult catch rates were low at these sites. To avoid bias in the results from tadpole samples representing offspring from only one breeding pair, tadpoles were sampled in different breeding ponds.

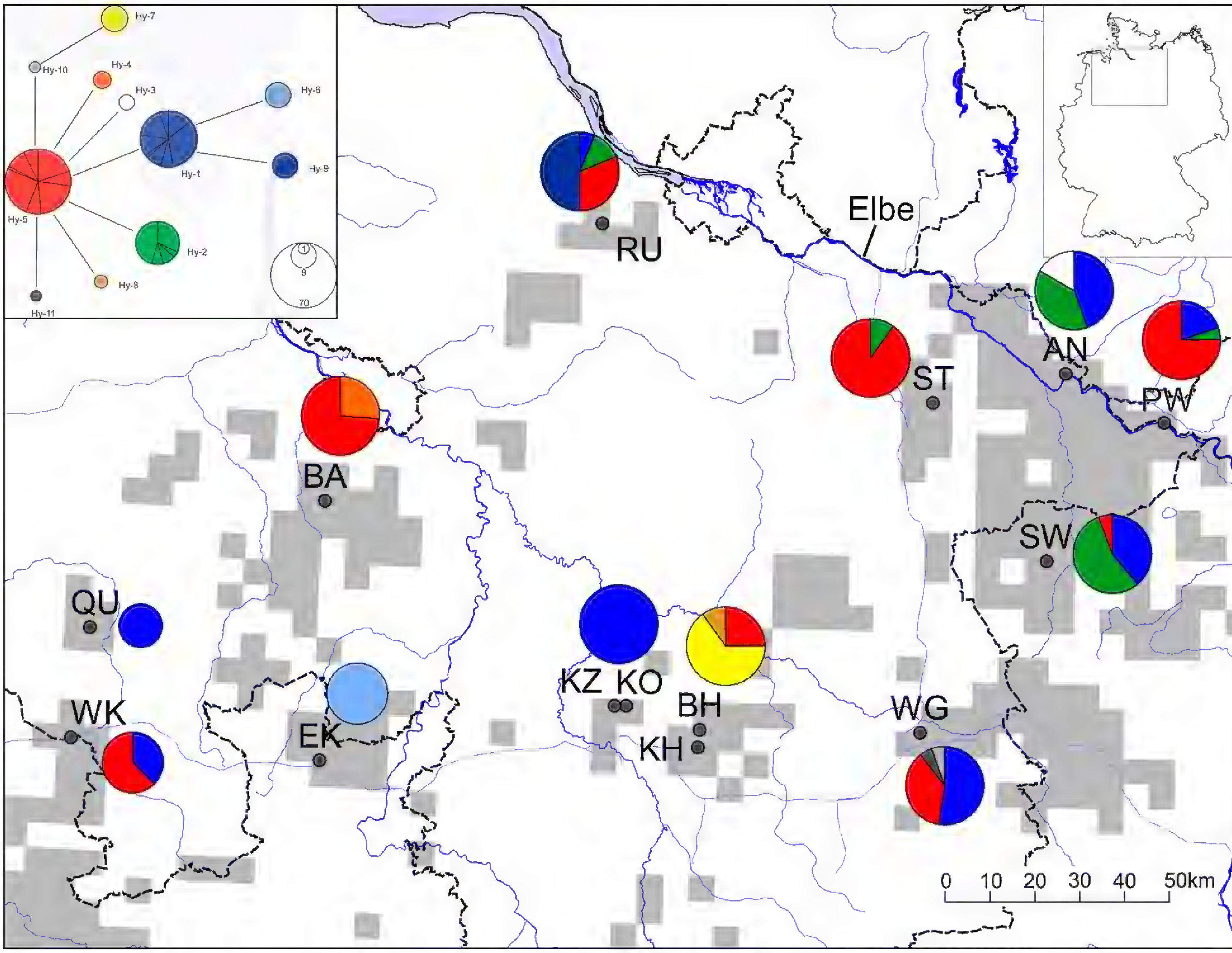

Fig. 1. Current distribution of the European Tree Frog, and the distribution of cyt *b* haplotypes in Lower Saxony and adjacent areas on the basis of TK25-quadrants (grey squares) during 1994–2010 in Lower Saxony (NLWKN 2011), 1993–2006 in North Rhine Westphalia (LANUV 2011), and 1990–2000 in Saxony Anhalt (Meyer et al. 2004). Dashed lines denote state borders, dots denote sample sites. **Inset in upper left corner:** Haplotype network of 11 distinct haplotypes of cyt *b* of *H. arborea* (901 bp) in Lower Saxony and adjacent areas. Each haplotype is represented by one circle and color. The size of a circle corresponds to the haplotype frequency. Lines between haplotypes denote mutational steps between sequences.

The genetic diversity for these localities was similar to other locations, suggesting that relatedness among samples did not bias the results (Table 1). DNA from the tail clips was fixed in 99% ethanol and extracted using a proteinase K digestion followed by a Phenol-Chloroform protocol (Sambrook et al. 1989), and then stored at -20 °C. DNA was extracted from the buccal swabs with an Invisorb Spin Swab Kit (Invitek) following the manufacturer's protocol, and stored at -20 °C. Another study confirmed that buccal swabbing is a very efficient method for obtaining DNA of adequate quality for microsatellite amplification (Broquet et al. 2007).

A total of seven polymorphic microsatellite loci (WHA1-9, WHA1-20, WHA1-25, WHA1-67, WHA1-103, WHA1-104, and WHA1-140) previously isolated by Arens et al. (2000) were amplified following the author's protocol, except that the annealing temperature for WHA1-20 was changed to 64.6 °C. The PCR products were genotyped using the capillary sequencer MegaBace 1000 (Amersham Bioscience). Allele scoring was performed using the software Genetic Profiler v. 2.2. The genotyping results can be found in the file that accompanies this article (Supplementary file 1).

Because earlier analyses (Stöck et al. 2012) included only four samples of mt DNA from Germany, we also sequenced cytochrome *b* (cyt *b*) fragments of 901 bp for 5–20 individuals from each sample site, excluding KO and BH from the Hannover population. The cyt *b* fragment was amplified via PCR using the primers MVZ 15-L (5'-GAACTAAT GGCCCA CACWWTACGNAA -3') and cyt *b* AR-H (TAWAAGGGTCTTCTACTGGTTG) from Moritz et al. (1992) and Goebel et al. (1999). The PCR reaction (25 µl) consisted of 20–100 ng DNA, 1 µl of each primer (10 µM), 0.8 µl dNTPs (10 mM, 5PRIME), 2.5 µl 10x advanced Buffer (5PRIME), 1.25 U Taq DNA Polymerase (5PRIME), and 17.45 µl H_2O. The PCR conditions were as follows: an initial denaturation at 94 °C for 3 min; 35 cycles at 94 °C for 45 s, annealing temperature of 50 °C for 45 s, and extension at 65 °C for 1 min. The PCR products were sent to the Macrogen Company (Seoul, South Korea) for purification and sequencing with an ABI3730XL genetic analyzer (Applied Biosystems).

Table 1. Overview of data from the various sample sites. [a]: Samples from adult frogs, [t]: samples from tadpoles, H_o: observed heterozygosity, H_e: expected heterozygosity, SD: standard deviation, F_{IS}: inbreeding coefficient, with bold values for significant differences after 1,000 permutations, R: mean allelic richness over all loci, *h*: haplotype diversity, π: nucleotide diversity, *N*: number of sampled individuals, N_A: mean number of alleles over all loci.

ID	Sample site	mean H_o ± SD	mean H_e ± SD	F_{IS}	N_A	R	*h*	π [%]	*N*
QU	Quakenbrück [a]	0.786 ± 0.248	0.741 ± 0.143	-0.070	4.00	–	0.00	0.00	5
WK	Westerkappeln [a]	0.661 ± 0.187	0.579 ± 0.158	**-0.154**	3.43	–	0.54	0.06	8
EK	Espelkamp [a]	0.796 ± 0.169	0.754 ± 0.087	-0.058	5.29	5.18	0.00	0.00	12
KZ	Kananohe Zentrum [a]	0.667 ± 0.169	0.666 ± 0.134	-0.001	5.14	4.65	0.00	0.00	20
KO	Kananohe Ost [a]	0.701 ± 0.208	0.684 ± 0.089	-0.027	4.57	4.53	–	–	11
KH	Kolshorn [a]	0.754 ± 0.131	0.713 ± 0.094	-0.059	6.29	5.37	0.53	0.13	20
BH	Beinhorn [a]	0.693 ± 0.089	0.693 ± 0.093	-0.001	5.57	4.84	–	–	20
BA	Bassum [t]	0.771 ± 0.099	0.748 ± 0.092	-0.032	5.43	4.98	0.41	0.05	20
RU	Ruschwedel [a]	0.731 ± 0.064	0.721 ± 0.050	-0.015	5.00	4.50	0.68	0.14	18
WG	Wolfsburg-Gifhorn [a]	0.790 ± 0.158	0.799 ± 0.080	-0.011	7.71	6.65	0.61	0.08	20
ST	Strothe [a/t]	0.735 ± 0.153	0.708 ± 0.126	-0.039	6.29	5.34	0.19	0.02	21
AN	Amt Neuhaus [a]	0.708 ± 0.111	0.750 ± 0.090	0.057	6.43	5.50	0.66	0.15	22
SW	Salzwedel [t]	0.600 ± 0.227	0.687 ± 0.181	**0.130**	6.00	5.01	0.57	0.11	20
PW	Pevestorfer Wiesen [a]	0.793 ± 0.110	0.764 ± 0.091	-0.039	6.43	5.55	0.42	0.05	20

Statistical Analysis

Analysis of mtDNA

Both directions of the cyt *b* sequences were assembled using the computer software SeqMan™ II (DNASTAR, Inc., Konstanz, Germany). Multiple sequence alignments were performed in MEGA 4 (Tamura et al. 2007) using the Muscle algorithm (Edgar 2004), and all variable sites were confirmed by visual inspection of the chromatograms. The EMBL-EBI sequence analytical tool (Madeira et al. 2022) was used to convert the sequences to the corresponding amino acid sequences in order to assure that nuclear copies were not sequenced. The program MEGA was applied to calculate *p*-distances between sample sites (Tamura et al. 2004). Haplotype diversity (*h*) and nucleotide diversity (π) (Nei 1987) were determined with Arlequin ver. 3.11 (Excoffier et al. 2005). A haplotype network of the cyt *b* data set was constructed via the statistical parsimony analysis of the program TCS 1.21 (Clement et al. 2000) using the default settings.

Analysis of Microsatellites

Microsatellite data were checked for null alleles, stuttering, and allelic dropout using Micro-Checker (Van Oosterhout et al. 2004). The program Fstat v. 2.9.3 (Goudet 1995) was used to test for genotypic disequilibrium of all pairs of loci in each sample and to calculate average allelic richness per population. For the calculation of average allelic richness, sample sites with less than ten individuals (QU and WK) were excluded.

For each sample site and locus, the observed and expected heterozygosity (Nei 1987) and deviation from Hardy-Weinberg equilibrium (HWE) (Guo and Thompson 1992) were determined with Arlequin ver. 3.11 (Excoffier et al. 2005). Genepop ver. 4.1 (Rousset 2008) was used to test for a global deviation from HWE in each sample site. The inbreeding coefficient F_{IS} per sample site (Weir and Cockerham 1984) was calculated using Genetix ver. 4.05 (Belkhir et al. 2004) and the significance was tested with a permutations test (1,000 permutations).

Genetic differentiation between the sample sites was calculated as global F_{ST} and pairwise F_{ST} values (Weir and Cockerham 1984) in Arlequin (Excoffier et al. 2005). In addition, pairwise D_{est} (Jost 2008), a substitute measure of genetic differentiation, was calculated using the R package DEMEtics (Gerlach et al. 2010). Significance was calculated by 10,000 bootstraps.

The data were also tested for Isolation By Distance in sampled populations (IBD; Storfer et al. 2010; Wright 1943). IBD occurs when gene flow occurs but declines with increasing distances between pairs of populations, and is typical for the genetic population structure of many animal species (Hitchings and Beebee 1997; Spear et al. 2005; Vergara et al. 2015). To test for IBD, a Mantel test for correlation between pairwise genetic distances (F_{ST} and D_{est}) and pairwise geographic distances was conducted, implemented in IBDWS 3.23 (Jensen et al. 2005). As proposed by Rousset (1997) for populations in two-dimensional habitats, geographical distance was log-transformed and genetic distance was expressed as F_{ST} /(1 − F_{ST}), and D_{est} /(1 − D_{est}). Significance for $r \geq 0$ was assessed via 10,000 bootstraps. The linear geographic distances among sample sites were calculated in ArcView GIS 3.3 using the Distance Matrix extension (Jenness 2005).

Even though the Mantel test is widely used in landscape genetic studies, an evaluation of different methods revealed that Mantel tests exhibit high type-1 error rates (Balkenhol et al. 2009). Those authors recommended applying a combination of statistical methods to avoid inaccurate conclusions derived from only one method. Therefore, two additional hierarchical Bayesian methods, GESTE (Foll and Gaggiotti 2006) and BIMr (Faubet and Gaggiotti 2008), were applied here for evaluating the effect of distance by means of generalized linear models. Both BIMr and GESTE perform well for moderate samples sizes and limited numbers of loci, as in our study (Balkenhol et al. 2009).

GESTE estimates the genetic distance (F_{ST} values) for each local population pair from multilocus genotypes and correlates them to environmental factors. Posterior probabilities associated with each factor allow the identification of factors with the highest effect on genetic structure. The regression coefficient estimate (Alpha) indicates whether a factor reduces or enhances genetic differentiation. The estimation of model parameters is performed by using a combination of Markov Chain Monte Carlo (MCMC) and Reversible-Jump MCMC (RJMCMC) (Green 1995). As environmental factors, we included latitude (G1) and longitude (G2; geographic coordinates in GK3 format) as approximations of the effect of distance among population pairs.

The software BIMr 1.1 estimates contemporary gene flow and assesses the influence of genetic distance on gene flow. This program quantifies the gametic disequilibrium from multilocus genotypes (here, microsatellite alleles) generated by the progeny of recent migrants to calculate the proportion of the population that immigrated during the last generation (Faubet and Gaggiotti 2008). Five replicates (= runs) were run with a total of 1,020,000 iterations (burn-in: 1,000,000, sample size: 20,000) and a thinning interval of 50 iterations. For each replicate, first 20 short pilot MCMC runs of 1,000 iterations were conducted, and the run with the lowest Bayesian deviance (D_{assign}) and the highest posterior probability was selected to extract the parameter estimates (Faubet et al. 2007; Faubet and Gaggiotti 2008). Two models were calculated: model 0 did not include environmental factors and model 1 included factor G1 which is the geographic distance between pairs of populations. As an alternative, the BayesAss software (Rannala 2007; http://www.rannala.org/software/) was also used to infer contemporary migrations rates. The software was run with 10,000,000 iterations (i), a burn-in (b) of 1,000,000 repetitions, and the interval between samples (n) was set to 1,000. The default values were used for all other parameters at first. Then, we adjusted the mixing parameters for migration rate (m), allele frequencies (a), and inbreeding coefficients (f) to maintain their acceptance rates between 20% and 60% as recommended in the Manual.

To infer genetic clusters, individual assignments to populations were conducted by means of a combination of non-spatial and spatial Bayesian algorithms with Structure version 2.3.3 (Pritchard et al. 2000) and TESS version 2.3 (Chen et al. 2007; François et al. 2006). Simulation data suggested the combination of TESS and Structure as a reliable approach for deducing the spatial population structure (Chen et al. 2007), outperforming other Bayesian clustering programs. All Structure runs used 500,000 iterations after a burn-in period of 100,000. An admixture ancestry model and correlated allele frequencies were used between populations. Structure was run both without and with information about the sampling location (prior population information) and the results were compared as recommended by Pritchard et al. (2000; see also Dufresnes et al. 2013; Olsen et al. 2014). Hierarchical analyses were performed by repeating the Structure runs with each of the major clusters. Twenty runs were conducted for each *K*. The range of possible *K*s tested spanned from 1 to 14, according to the number of sampled breeding sites. The average log likelihood Pr(X|*K*) (given by the estimated Ln Prob of data = Ln P(D) in the software result output, see Table 4) was calculated for each *K* across all runs. Since detecting the true number of *K* is not always straightforward, we included the ΔK statistics proposed by Evanno et al. (2005), using Structure Harvester v.0.6.8 (Earl and von Holdt 2012).

TESS uses a Bayesian method to detect population structure, but it considers the spatial information (geographical coordinates) of the individuals. After assessing the preliminary runs as recommended in the software manual, the maximum number of allowed genetic clusters (K_{max}) was varied from 2 to 10. One hundred independent runs for each K_{max} were conducted under the admixture model, with 50,000 sweeps and a burn-in period of 10,000 sweeps for each run.

Finally, the NeEstimator v2 software was used to estimate the contemporary effective population sizes at all sample sites (Do et al. 2014). Three single sample estimators were implemented: the linkage disequilibrium method, the heterozygote-excess method, and the molecular coancestry method. The lowest allele frequencies (P_{Crit}) were set to 0.05, 0.02, 0.01, and 0+.

Results

Genetic Diversity

Genetic diversity was estimated for each population based on the microsatellite alleles and the cyt *b* haplotypes (Table 1). While genetic diversity indices based on microsatellites (H_o, H_e, N_A, and R) are moderate to high across the range, they are always highest in WG (except for H_o); while the indices based on cyt *b* (*h*, π) tend to increase from west (WK/QU) to east (PW) (Table 1; Fig. 1).

Table 2. Pairwise D_{est} values (lower matrix) and pairwise F_{ST} values (upper matrix) between sample sites; ns = not significant. See Table 1 for sample site acronym definitions.

	QU	WK	EK	KZ	KO	KH	BH	BA	RU	WG	ST	AN	SW	PW
QU	0	0.120	0.066	0.111	0.113	0.110	0.103	0.039	0.117	0.043	0.086	0.086	0.084	0.052
WK	0.208	0	0.114	0.064	0.107	0.117	0.154	0.097	0.191	0.107	0.083	0.119	0.162	0.147
EK	0.195	0.286	0	0.041	0.031^{ns}	0.069	0.076	0.060	0.090	0.061	0.095	0.065	0.097	0.071
KZ	0.284	0.145	0.102	0	0.002^{ns}	0.090	0.099	0.066	0.139	0.081	0.092	0.081	0.095	0.105
KO	0.324	0.243	0.097	0.001^{ns}	0	0.092	0.104	0.059	0.130	0.081	0.092	0.074	0.091	0.106
KH	0.412	0.301	0.222	0.279	0.290	0	0.025	0.053	0.062	0.064	0.056	0.074	0.110	0.094
BH	0.387	0.372	0.230	0.284	0.311	0.059	0	0.074	0.092	0.082	0.076	0.102	0.118	0.100
BA	0.189	0.230	0.220	0.199	0.189	0.172	0.225	0	0.074	0.037	0.072	0.070	0.083	0.066
RU	0.424	0.449	0.285	0.382	0.386	0.173	0.252	0.235	0	0.068	0.079	0.072	0.110	0.073
WG	0.139	0.309	0.296	0.230	0.306	0.237	0.283	0.142	0.252	0	0.056	0.071	0.086	0.061
ST	0.299	0.208	0.329	0.281	0.308	0.175	0.238	0.239	0.222	0.201	0	0.057	0.110	0.070
AN	0.265	0.315	0.230	0.248	0.263	0.245	0.316	0.242	0.238	0.290	0.211	0	0.097	0.065
SW	0.238	0.391	0.289	0.233	0.228	0.368	0.367	0.272	0.347	0.287	0.369	0.343	0	0.078
PW	0.213	0.365	0.278	0.278	0.322	0.350	0.337	0.253	0.267	0.249	0.226	0.241	0.253	0

Mitochondrial Sequence Analysis

The analysis revealed 11 haplotypes of the cytochrome *b* fragment which differed by ten variable sites and nine parsimony informative sites (Fig. 1). There was no evidence for any diverged haplotype groups that would correspond to different genetic lineages. Most haplotypes were closely related but unique to one sample site, except for haplotypes Hy-1, Hy-2, and Hy-5. While Hy-1 (blue) and Hy-5 (red) showed a broad distribution over almost the complete sampling area, Haplotype Hy-2 (green) was restricted to five sample sites in the northeast (Fig. 1). Eight haplotypes were found at only a single locality: Hy-3 (white) in AN, Hy-4 (orange) in BA, Hy-6 (light blue) in EK, Hy-7 (yellow) and HY-8 (brown) in KH, Hy-9 (dark blue) in RU, and Hy-10 (grey) and Hy-11 (dark grey) in WG. In WG and RU, four different haplotypes were detected, while in QU, EK, and KZ (all in the west of Hannover) only one haplotype was found. The *p*-distances among localities were low, varying between 0 and 0.4 % (Supplementary Table S1). The GenBank accession numbers can be found in Supplementary Table S3.

Microsatellite Analysis

The seven microsatellite markers examined were polymorphic with seven to 16 alleles per locus. The analysis with Micro-Checker uncovered signs of null alleles for locus WHA1-67 in sample site KO and for locus WHA1-140 in sample site SW. As null alleles for these two loci were found at only a single sample site, we did not adjust for null alleles. Furthermore, this analysis revealed no evidence for large allele dropout or scoring errors due to stuttering.

Deviation from Hardy-Weinberg-Equilibrium (HWE) was found for WHA1-104, with a significant excess of heterozygotes in sample site KH. The global test for HWE over all loci in each population resulted in no significant deviation from HWE. Significance values for the inbreeding coefficient F_{IS} were obtained for the sample sites SW (F_{IS} = 0.130) and WK (F_{IS} = -0.154, Table 1). No linkage (genetic) disequilibrium was found between any pair of loci.

The global F_{ST} value across all localities was 0.083 and highly significant ($P > 0.0001$). Genetic differentiation calculated as pairwise D_{est} and pairwise F_{ST} values were significant in all cases except between the two sample sites in the West of Hannover (KZ and KO), as well as EK and KO regarding the F_{ST} values (Table 2). The Mantel test for IBD showed a significant but low correlation between the genetic and geographic distances (Fig. 2; D_{est}: $r = 0.28$, $P = 0.0117$; F_{ST}: $r = 0.29$, $P = 0.0145$, see also Supplementary Table S2), indicating that genetic differentiation is only partially explained by geographic distances among the sites.

GESTE calculated five different models (Table 3). The probability of a model was not improved by including either latitude (G1) or longitude (G2) without interaction. The model with the highest posterior probability was model 4, which included the constant, latitude, and longitude as well as their interaction. The Alpha values were low for the effects of both factors, while the Alpha value of the interaction indicates a significant effect on genetic differentiation.

All five replicates of the BIMr analysis showed a D_{assign} of 0.0. The highest posterior probability for the null model was 0.79 (run 1), and the lowest was 0.55 (run 4). The posterior probabilities for model 1 (including G1) were lower than the posterior probabilities of the null model (Table 4); i.e., the geographic distance did not seem to affect recent gene flow or migration among sample sites. Mean migration rates were extremely low and varied from 2.88e^{-12} to 1.11e^{-9}; while the highest mean migration rate was observed among PW and WG, and the lowest was among AN and QU. Also, the

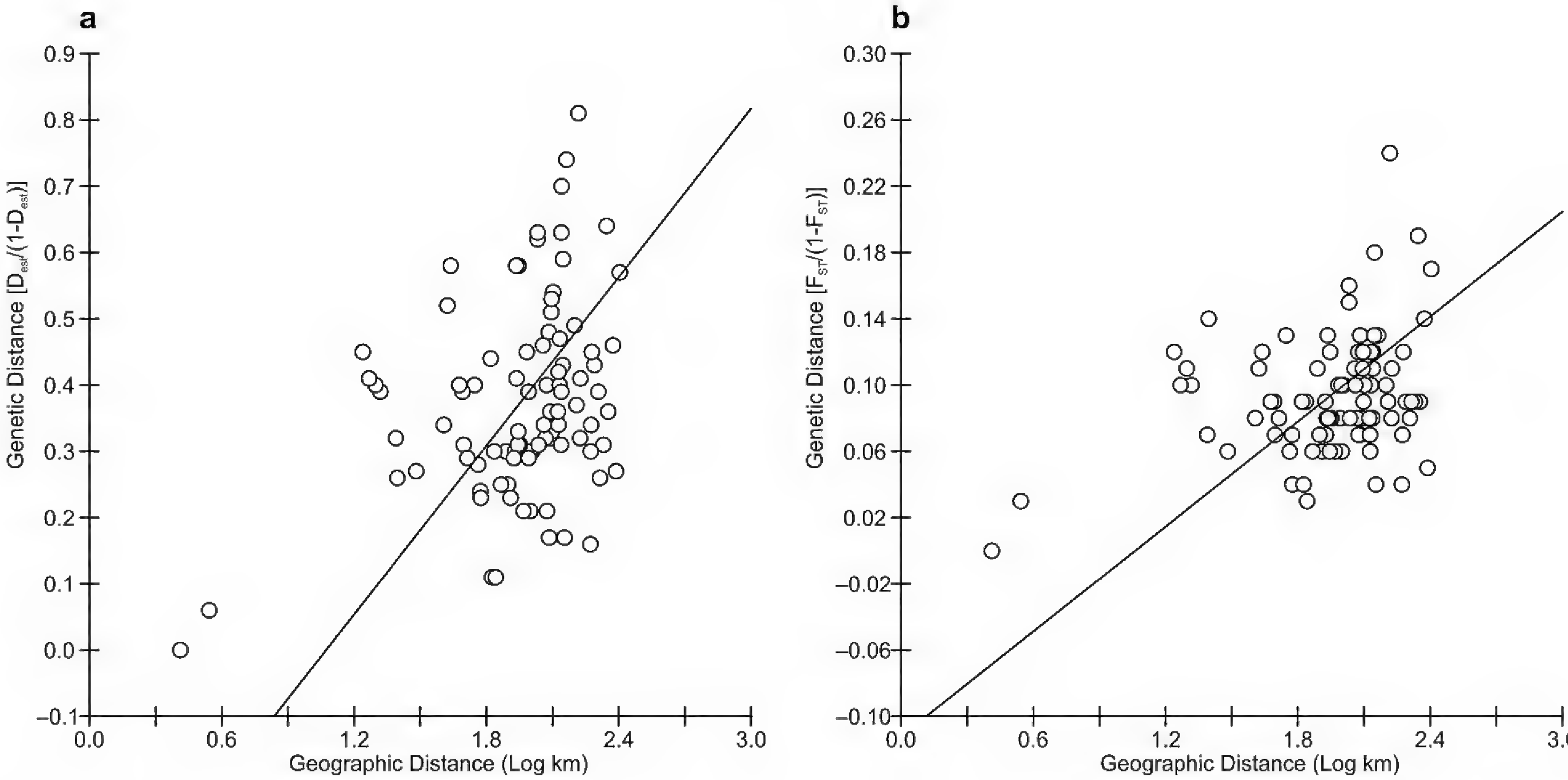

Fig. 2. Isolation By Distance plots. (a) $D_{est}/(1 - D_{est})$ versus log geographic distance; and (b) $F_{ST}/(1 - F_{ST})$ versus log geographic distance. The lines are the RMA (Reduced Major Axis) regressions.

migration rates between two close population pairs in the surroundings of Hannover were very low. For example, the mean migration rates between KH to BH and vice versa were only 1.66e^{-10} and 2.34e^{-10}, and those between KZ and KO were 1.92e^{-10} and 2.24e^{-10} even though the distances between these pairs were only 3.94 km and 2.6 km, respectively. The analysis with BayesAss provided very similar results for the runs with default and adjusted parameters. The migration rates were higher than those calculated with BIMr, most of which fluctuated around 0.01. Interestingly, the migration rates between EK and KZ, KO and KZ, as well as KH and BH were considerably higher (0.14, 0.16, and 0.20, respectively) and more consistent with the genetic population structure (Fig. 3) as well as the above-mentioned geographic distances.

Bayesian assignments conducted by Structure suggested two major groups (K = 2), separating the western/central populations (WK-BA-EK-KZ-KO-BH-KH) and the northern/eastern populations (RU-WG-ST-AN-PW-SW, Figs. 3A and 4, see also Supplementary Fig. S1A). The population QU appeared to be admixed, but was unambiguously assigned to the western group by TESS (see below). Within each cluster, a fine substructuring could be detected, and the two approaches (with/without prior population information) provided slightly different clustering solutions. In those runs where the sampling location was used as prior information, the western/central cluster was split along Hannover with some admixed populations in the western part of the region (K = 3, Fig. 3B). The Structure runs without prior population information supported the existence of two genetic subclusters within this region (Supplementary Fig. S1B). In the northern/eastern cluster, both approaches provided similar results (Fig. 3C and Supplementary Fig. S1C). RU was differentiated from WG and ST, which in turn differed from the populations lying in the eastern part of the study area in Saxony Anhalt. More detailed results of log likelihood Pr(X|K) values and ΔK statistics are provided in the Supplementary figures (Figs. S2 and S3, respectively).

The TESS analysis supported the two major genetic groups separated into a western/central cluster and a northern/eastern cluster (Fig. 5). Increasing the number of K_{max} resulted in only a slight decrease in the Deviance

Table 3. Posterior probabilities for five possible models calculated with GESTE explaining the genetic differentiation of European Tree Frogs as a function of the environmental factors latitude (G1) and longitude (G2). Constant is the intercept of the regression model. The regression coefficients (Alpha) for different environmental factors used in the models are given in the right side of the table.

Model	Factors included	Posterior probability	Factors	Regression coefficients	
Model 0	Constant	0.19	Constant	Alpha 0	-3.69
Model 1	Constant, G1	0.19	G1	Alpha 1	0.06
Model 2	Constant, G2	0.18	G2	Alpha 2	-0.07
Model 3	Constant, G1, G2	0.17	G1*G2	Alpha 3	-2.14
Model 4	Constant, G1, G2, G1*G2	0.26			

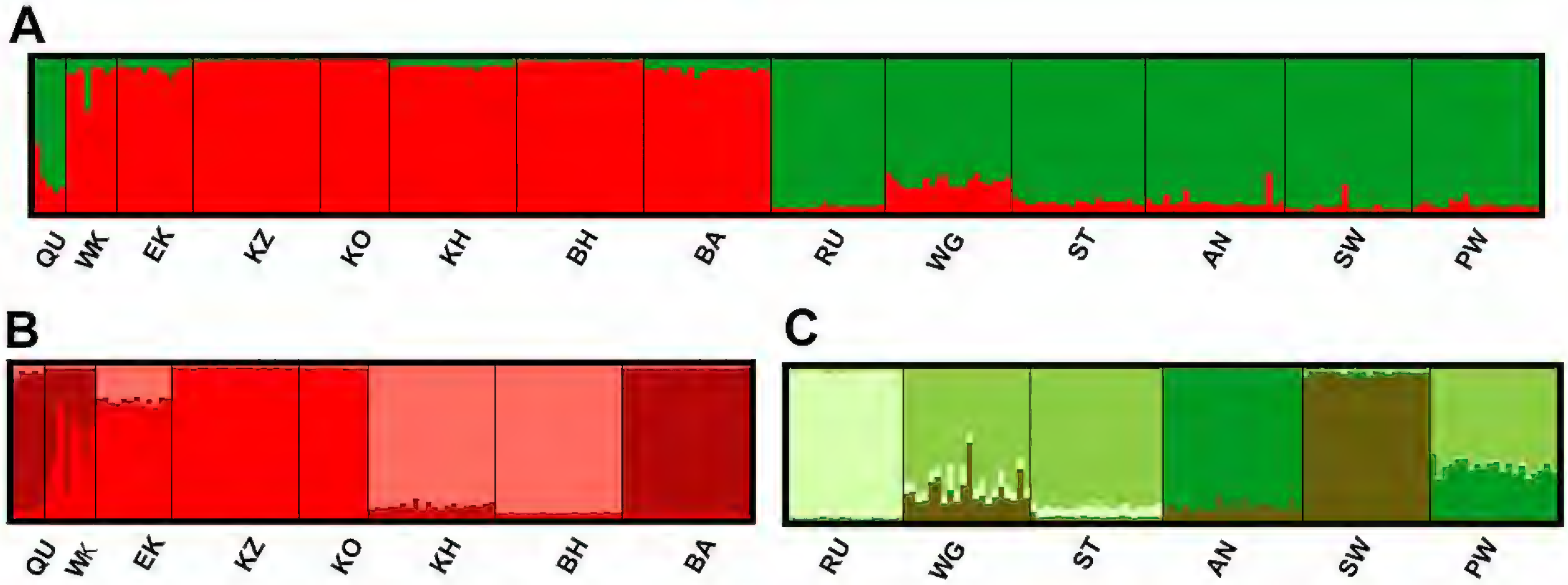

Fig. 3. Estimation of the number of *Hyla arborea* populations using the program STRUCTURE ver 2.3.1 (Pritchard et al. 2000) for the admixture model with prior population information; QU, WK, EK, etc. = sample sites, separated by fine black lines. Each individual is represented by a single vertical line broken into colored segments, with lengths proportional to the corresponding clusters. (A) Plot for $K = 2$ in the analysis of the entire data set, (B) plot for $K = 3$, and (C) $K = 4$ for hierarchical analysis on each of the two main clusters.

Information Criterion (DIC) of the models while the resulting population structure was not consistent among runs for each K_{max} or in comparison with the STRUCTURE results (data not shown). STRUCTURE as well as TESS revealed that frogs from WG in the eastern group (Fig. 3A) are of admixed origin from both genetic groups as the assignment results from the two were similar.

Effective Population Sizes

Mean effective population sizes (N_e) varied among the sample sites and statistical methods applied. The results also differed between $P_{Crit} = 0.05$ and the other P_{Crit} but were the same for $P_{Crit} = 0.02$, 0.01, and 0+ (Table 5). The large confidence intervals indicate that the results might not be very reliable. However, most calculated N_e values were small (100 individuals or less). Only three sample sites (KO, AN, and PW) showed consistently high values for N_e (500 or higher, or infinite) for most methods.

Discussion

The analyses presented here provide valuable information for the conservation management of the Endangered European Tree Frog species, *Hyla arborea*, which suffers from population isolation in its northern distribution range. In Lower Saxony, a weak correlation between genetic and geographic distances suggests a low level of recent gene flow among localities, and further analyses indicate a lack of current migration at least during the last generation. Two major genetic clusters, one in the east and one in the west, were found with some admixture in a central population. Both main clusters were further subdivided into several distinct regional clusters. The substantial population structure, verified by significant genetic distances among localities, suggests that the populations are currently isolated to a large extent. Consequently, conservation management is needed to ensure the long-term persistence of this species in Lower Saxony with suitable effective population sizes and high levels of genetic diversity that are necessary to counteract the reductions in fitness and adaptive potential (Andersen et al. 2004; Frankham 2005; Allentoft and O'Brien 2010; Angelone 2010).

Isolation by Geographic and Genetic Distances

In addition to the Mantel test, the landscape genetic analysis in GESTE provided some insight into the role of geographic distance on genetic differentiation. While the models including latitude and longitude alone did not offer a better explanation for genetic differentiation than the null model, the most complex model including the interactions between latitude and longitude did. We interpret this as the effect of the geographic distance

Table 4. Results of BIMr analysis (means of posterior probability and Alpha for run 1) for estimating migration rates among localities with European Tree Frogs in Lower Saxony. The factor G1 is the geographic distance. Alpha 0 and Alpha 1 represent estimates of the constant term and factor G1, respectively.

Model	Factor	Posterior probability	Alpha 0	Alpha 1
Model 0		0.79	1.64	
Model 1	G1 = geographic distance	0.21	1.48	0.14

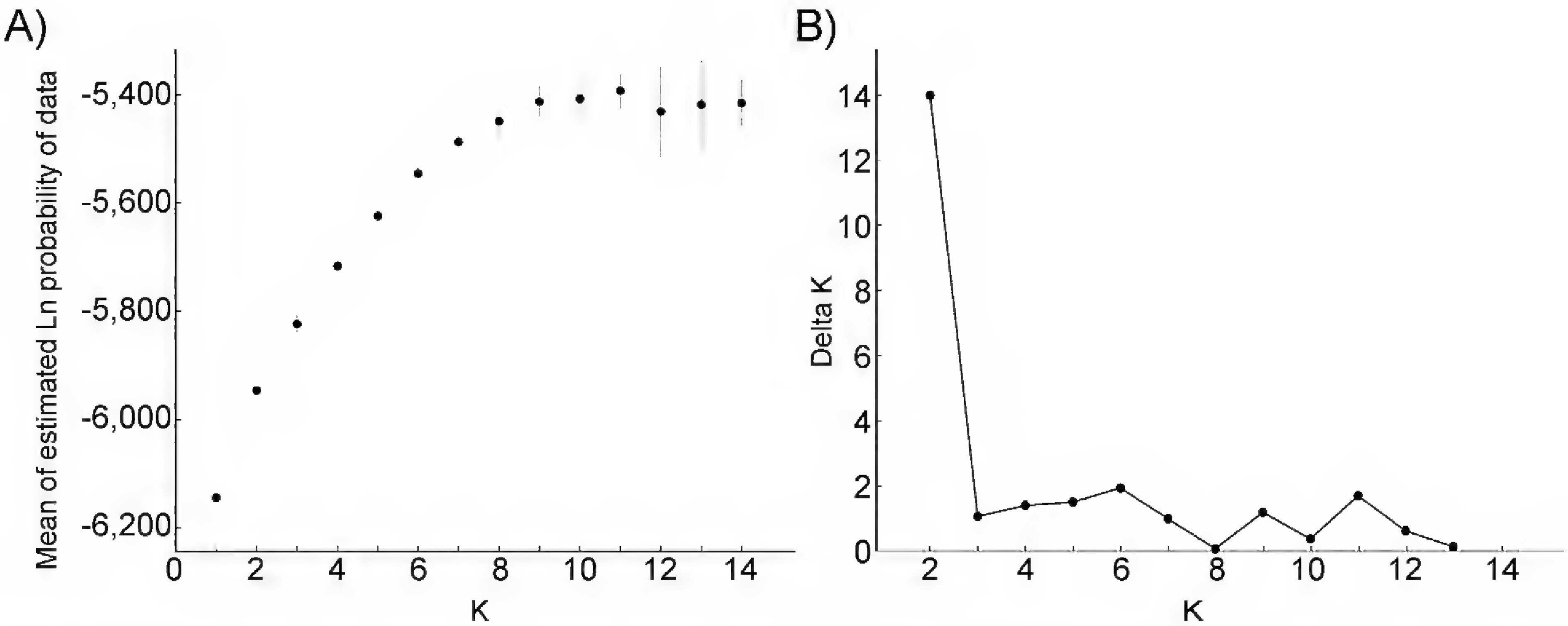

Fig. 4. Mean values of estimated Ln probability of data (LnPD) for each *K* (a) and delta *K* (b) when prior population information was implemented.

on genetic dissimilarity between localities. Overall, however, the posterior probability and alpha values illustrate that the distance effect is not very large. Habitat fragmentation might play a more important role in shaping the genetic structure of the tree frogs in this area. According to Podloucky and Fischer (2013), habitat fragmentation in Lower Saxony is mainly caused by the loss of summer habitat, breeding ponds, and corridors suitable for migration. This is in accordance with the disconnected distribution (Fig. 1) and significant genetic distances (F_{ST} and D_{est}) among most tree frog populations.

A significant population structure as a result of limited dispersal between isolated populations is typically accompanied by a slight to moderate effect of isolation by distance. Isolation by distance was detected in some European amphibian species (*Rana dalmatina*, Sarasola-Puente et al. 2012; *Bombina variegata*: Weihmann et al. 2009; Hantzschmann et al. 2020), but not others (*Bufo calamita*: Allentoft et al. 2009; *Bombina bombina*: Dolgener et al. 2012). For the tree frogs in Lower Saxony, the small positive correlation ($r \sim 0.28$) between genetic and geographic distances suggests a very low level of recent gene flow among localities. This finding is in accordance with earlier studies on tree frogs, which reported small to moderate correlation coefficients between both distances and significant population structure (Andersen et al. 2004; Angelone and Holderegger 2009; Arens et al. 2006). In all these studies, limited gene flow was explained by habitat fragmentation, particularly the loss of breeding ponds. In contrast, in those frog species which occur in more continuous habitats or that have higher dispersal capacities, the

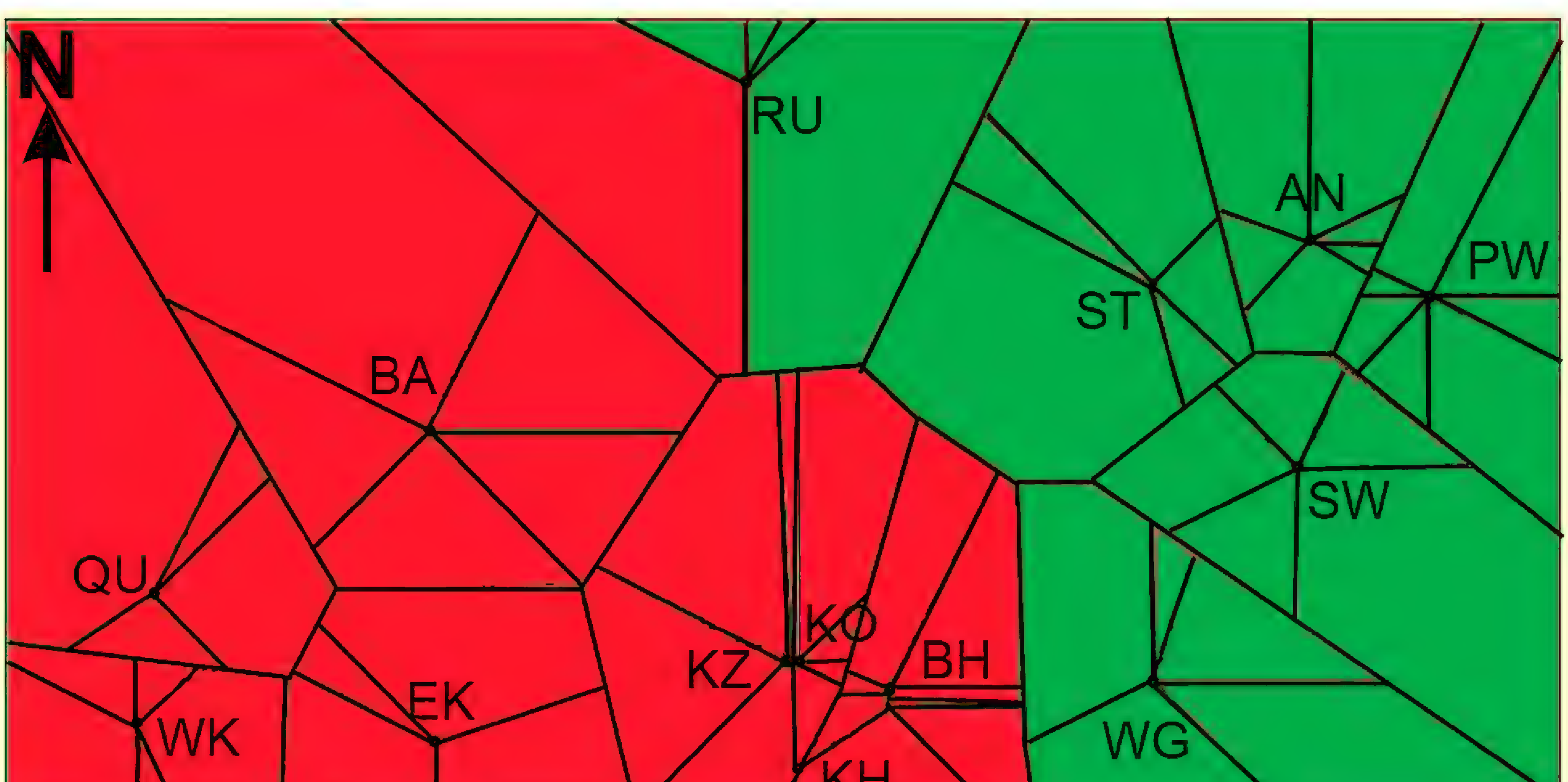

Fig. 5. Map of geographic-genetic cluster membership for $K_{max} = 2$ as inferred by TESS.

Table 5. Results for effective populations sizes (N_e) calculated with the N_e Estimator for three different methods and different P_{Crit} values. N_e values were the same for P_{Crit} = 0.02, 0.01, and 0+. Only 0+ is used in the Molecular Coancestry method. Mean values (N_e) and Confidence Intervals (CIs) are given for each sample site, method, and P_{Crit} option.

		The three methods				
		Linkage disequilibrium		Heterozygote excess		Molecular coancestry
Sample site	P_{Crit}	0.05	0.02/0.01/0+	0.05	0.02/0.01/0+	0+
QU	N_e	55.7	55.7	7.8	7.8	9.5
	CIs	1.4 – inf.	1.4 – inf.	3.7 – inf.	3.7 – inf.	5.1 – 15.2
WK	N_e	1.3	1.3	5.1	5.1	2.7
	CIs	0.7 – 2.7	0.7 – 2.7	2.5 – inf.	2.5 – inf.	2.0 – 3.5
EK	N_e	16.3	33.5	9.9	9.9	8.2
	CIs	5.6 – inf.	8.7 – inf.	4.5 – inf.	4.5 – inf.	2.7 – 16.9
KZ	N_e	46.3	28.2	34.7	34.7	5.6
	CIs	15.8 – inf.	12.1 – 319.2	7.5 – inf.	7.5 – inf.	2.3 – 10.5
KO	N_e	inf.	611.3	251.5	251.5	inf.
	CIs	11.4 – inf.	10.4 – inf.	4.3 – inf.	4.3 – inf.	inf. – inf.
KH	N_e	319.3	159.7	inf.	44.3	5.7
	CIs	30.5 – inf.	30.2 – inf.	5.8 – inf.	6.0 – inf.	3.2 – 8.9
BH	N_e	83.5	73.5	731.7	inf.	inf.
	CIs	21.0 – inf.	21.3 – inf.	7.2 – inf.	7.7 – inf.	inf. – inf.
BA	N_e	177.2	188.0	322.0	322.0	10.8
	CIs	26.5 – inf.	26.8. inf.	6.5 – inf.	6.5 – inf.	1.8 – 27.7
RU	N_e	19.3	27.5	67.7	81.9	inf.
	CIs	8.4 – 106.4	10.8 – inf.	6.8 – inf.	7.1 – inf.	inf.
WG	N_e	31.1	65.5	inf.	inf.	9.1
	CIs	16.0 – 113.5	26.0 – inf.	8.1 – inf.	9.3 – inf.	3.8 – 16.6
ST	N_e	34.7	77.5	39.7	51.0	inf.
	CIs	15.7 – 315.7	25.4 – inf.	6.4 – inf.	7.2 – inf.	inf. – inf.
AN	N_e	inf.	inf.	inf.	inf.	inf.
	CIs	41.7 – inf.	74.0 – inf.	30.9 – inf.	57.8 – inf.	inf. – inf.
SW	N_e	37.3	36.0	inf.	inf.	43.4
	CIs	15.2 – inf.	16.1 – inf.	inf. – inf.	280 – inf.	0 – 217.7
PW	N_e	631.9	inf.	inf.	inf.	inf.
	CIs	36.2 – inf.	73.1 – inf.	6.1 – inf.	6.6 – inf.	inf. – inf.

correlation between geographic and genetic distance is higher (e.g., Pröhl et al. 2006) or disappears in case of panmixia (Leblois et al. 2000).

The BIMr analysis revealed that contemporary migration (i.e., during the last generation) was practically absent among the sample sites of tree frogs in Lower Saxony. This is in contrast to the migration rates calculated with BayesAss and the results of the Structure analysis (see below), which imply that individuals of mixed ancestry exist in the different genetic clusters. However, gene flow over the last few tree frog generations may have suffered due to the expanding habitat fragmentation, while some decades ago far more tree frog localities were reported for lower Saxony, thus, the connectivity among them was much better (Manzke and Podloucky 1995). Therefore, the signals for gene flow are still apparent in the results of some analyses (Structure, BayesAss) but not in those where the calculations are restricted to the most recent years (BIMr).

Genetic Diversity

The expected microsatellite heterozygosity (H_e) has been measured in a number of previous population genetic studies of the European Tree Frog. Interestingly, H_e was higher in the current study area (H_e: 0.60 – 0.79) than in most other northern areas where the genetic situation of the tree frog was investigated (e.g., H_e values in Denmark: 0.35–0.54, Andersen et al. 2004; Switzerland: 0.27–0.71, Angelone and Holderegger 2009; and the Netherlands:

0.39–0.59, Arens et al. 2006). As expected, the more peripheral populations, such as those in Denmark and the Netherlands, show lower genetic diversity values. In comparison, the *mt*haplotypes diversity (mean $h = 0.38$, $n = 14$ populations) is lower in the Lower Saxony area than in the southern part of the distribution range (Greece, Albania, Croatia, Serbia, and Romania) were the average h amounts to 0.7 ($n = 20$ populations, calculated from Dufresnes et al. 2013, Table S2). From all cumulative data within the framework of this study, we can conclude that in central and northern Europe, human induced fragmentation processes involving habitat destruction in a previously widely distributed frog species are contributing to the depletion of genetic diversity.

Genetic Structure and Conservation Units

The Bayesian cluster analyses conducted with Structure and TESS support the division of the tree frog populations into two major geographic-genetic clusters, one in the west and one in the east. One population in the south-east of the area (WG) shows admixture between the two groups and therefore a relatively high genetic diversity. Thus, it seems that both groups were previously connected by migrating animals when habitat fragmentation was less severe. This result is consistent with the moderate correlation between geographic distance and genetic distances. Both analyses also provide evidence for further fragmentation within both groups. In contrast, the haplotype network does not indicate any older, distinct (e.g., postglacial) lineages supporting the finding of Dufresnes et al. (2013), that only one evolutionary unit is present in this area.

Microsatellite pairwise D_{est} and F_{ST} values all showed significant genetic differentiation except for the two closest sites (KZ and KO) in the West of Hannover. However, *mt*haplotype distribution and Bayesian analyses of the microsatellites suggest distinct relationships among the currently fragmented localities. In the Northeast of Lower Saxony, the distribution of the *mt*haplotypes indicates a former connection of the populations along the river Elbe. Interestingly, the easternmost occurrences at AN, PW, and SW in the current and former distributions display a relatively well-connected area, nonetheless the presently distinct genetic sub-clusters in the Bayesian analyses and pairwise F_{ST} values are relatively high. The significant F_{IS} value found for SW indicates that the separation of this site may have resulted in inbreeding in an isolated population. Altogether, the available microsatellite data point to recent fragmentation of tree frog populations in this area, while similar *mt*haplotypes provide some evidence for a former connection.

Interestingly, there is a significant genetic divergence between the sample sites KZ and KO in the West and the sample sites KH and BH in the East of Hannover. One possible explanation is that recently constructed motorways in combination with genetic drift contributed to population differentiations, which are also apparent in the *mt*haplotype frequencies. Roads have been identified as barriers to gene flow in some other amphibians (Arens et al. 2007; Lesbarrères et al. 2006). One central question is whether these relatively young barriers (motorways expanding in the 1960s, and dense urban areas) are the only reason for the differentiation of these formerly linked tree frog localities (Manzke and Podloucky 1995). The low haplotype diversity in KZ, EK, and QU points to a loss of genetic diversity as a consequence of increased genetic drift in isolated occurrences.

In summary, the genetic analyses point to a highly structured population, as was observed in other surveys of European amphibians (Dolgener et al. 2012; Rowe and Beebee 2007; Sarasola-Puente et al. 2012; Hantzmann et al. 2020). The risks of fragmentation include population reduction, loss of genetic diversity and declining fitness, and finally extinction (Hitchings and Beebee 1997; Cushman 2006). To reverse such negative processes, conservation management that takes the genetic population structure into account is important (Allentoft et al. 2009; Olsen et al. 2014). For this endangered and fragmented frog species, we suggest delineating the two major genetic clusters as conservation units; and then within those, intense reconnection efforts should be undertaken by creating suitable habitats for migrating frogs. Moreover, there is clear evidence of admixture in WG, and gene flow along this route could be reestablished between both clusters.

Conservation Measures

In our opinion, future conservation management should be directed towards two aims. The first aim is to maintain high genetic diversity in large and stable populations within each conservation unit. In this context, it has been argued that an effective breeding size (N_e) of at least 50 animals is necessary to avoid inbreeding in the short term and that an N_e of 500 is necessary to maintain the evolutionary potential that would allow adaptations to environmental changes and assure long term viability (Jamieson and Allendorf 2012). Most of our isolated sample sites (e.g., BA, Fig. 3B–C) or sub-clusters (e.g., KH-BH) do not reach these effective population sizes. For tree frogs, the ratio of effective breeding size (N_e) to census size (N) is ~ 0.5 (Broquet et al. 2009). Therefore, we recommend the monitoring of population sizes and maintaining population sizes of at least 100 breeding frogs in isolated populations, i.e., each sub-cluster, for short term conservation goals, but increasing the population sizes to 1,000 or more embedded in each of several meta-population systems in every conservation unit (see also Andersen et al. 2004; Frankham et al. 2014). In cases where populations within a conservation unit are genetically and geographically separated, genetic rescue can be attained by establishing corridors to stimulate dispersal (e.g., in AN-SW-PW). Dense networks of suitable spawning

ponds have been destroyed by habitat conversion but are of great importance for the maintenance of large tree frog populations and the connection of subpopulations. There are several reports that tree frogs not only respond well to new suitable water bodies, but also depend on them for migrations exceeding several km and often colonize them in subsequent breeding seasons (e.g., Angelone and Holderegger 2009; Brandt and Lüers 2017; Hansen 2004; Schwartze 2002; Zumbach 2004).

The second aim is to maintain overall genetic diversity among the genetic clusters within the species and to protect local co-adapted gene complexes (Savolainen et al. 2013). To achieve this second goal, we recommend the re-establishment of gene flow between genetic clusters where possible, but at a lower level than within them. This particularly applies to the western and eastern clusters between which (former) gene flow is evidenced by the Structure analysis (Fig. 3). Habitat reconnection between these areas would allow a few frogs to travel between the breeding ponds of different clusters, thereby refreshing genetic diversity and counterbalancing the loss of genetic diversity through drift, while diverse selection pressures would sustain local adaptation. Levels of genetic diversity inferred from neutral markers are not necessarily correlated with variation in locally adapted traits. In this context, more research is necessary to understand which traits are locally adapted and how their variation affects the fitness of a population. Very isolated and small populations might benefit from translocations, i.e., the introduction of individuals from other populations. In such cases, translocations should be restricted to within the conservation unit to avoid causing outbreeding depressions that have sometimes been observed between distantly related populations (Sagvik et al. 2005).

Conclusions

Populations of the European Tree Frog in Lower Saxony are highly fragmented geographically and genetically, and therefore endangered. We identified two major genetic clusters and recommend that they should be considered as local conservation units. Conservation efforts should entail a reconnection of the populations within these conservation units, and to a lesser degree between them. Moreover, the maintenance of large and stable meta-populations within genetic sub-clusters (mostly consisting of isolated populations) needs to be achieved for long-term survival. For translocations of individuals to recovering very small and inbred populations or for reintroduction, we suggest a mixing of individuals from different populations within the same conservation unit to increase genetic diversity and enhance the adaptive capacity regarding changing environmental conditions. This study offers one example of how population genetic studies can help to delineate conservation units, and our recommendations might apply just as well to other endangered species where declines are connected to increasing habitat fragmentation.

Acknowledgements.—This research was supported by grants from the German Federal Environmental Foundation (DBU), Heidehof-Stiftung, and Hans-Schiemenz-Fonds - Deutsche Gesellschaft für Herp-etologie und Terrarienkunde (DGHT). We thank the following nature conservation authorities for permission to collect the tree frogs: Kreis Minden Lübbecke, Kreis Steinfurt, Landkreis Diepholz, Landkreis Gifhorn, Landkreis Lüneburg, Landkreis Osnabrück, Landkreis Stade, Landkreis Uelzen, Region Hannover, and Stadt Wolfsburg. We are especially grateful to the many people who helped during field work, and R. Podloucky for providing distribution maps. Finally, we thank our technician Sabine Sippel for her assistance in the molecular lab, Sönke von den Berg for help by creating the figures, Tjard Bergmann for submitting the Cyt *b* sequences to Genbank, and Oscar Gaggiotti for providing advice on BIMr.

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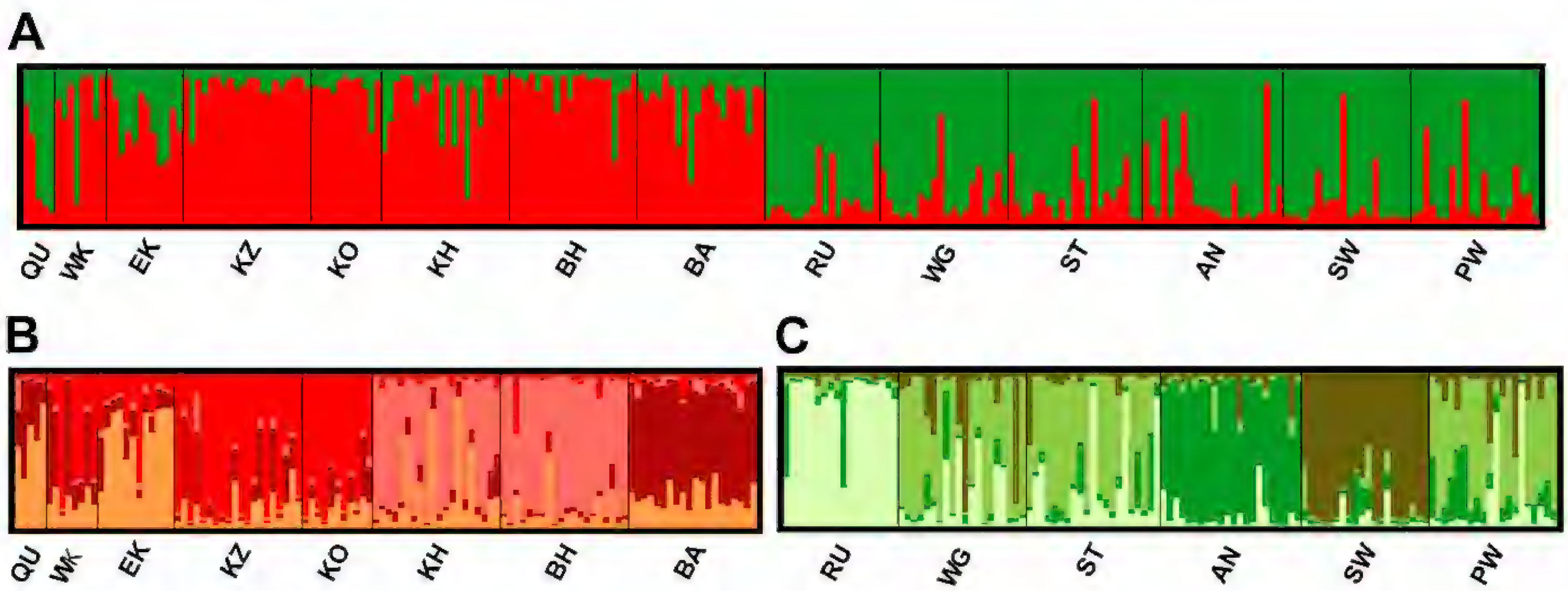
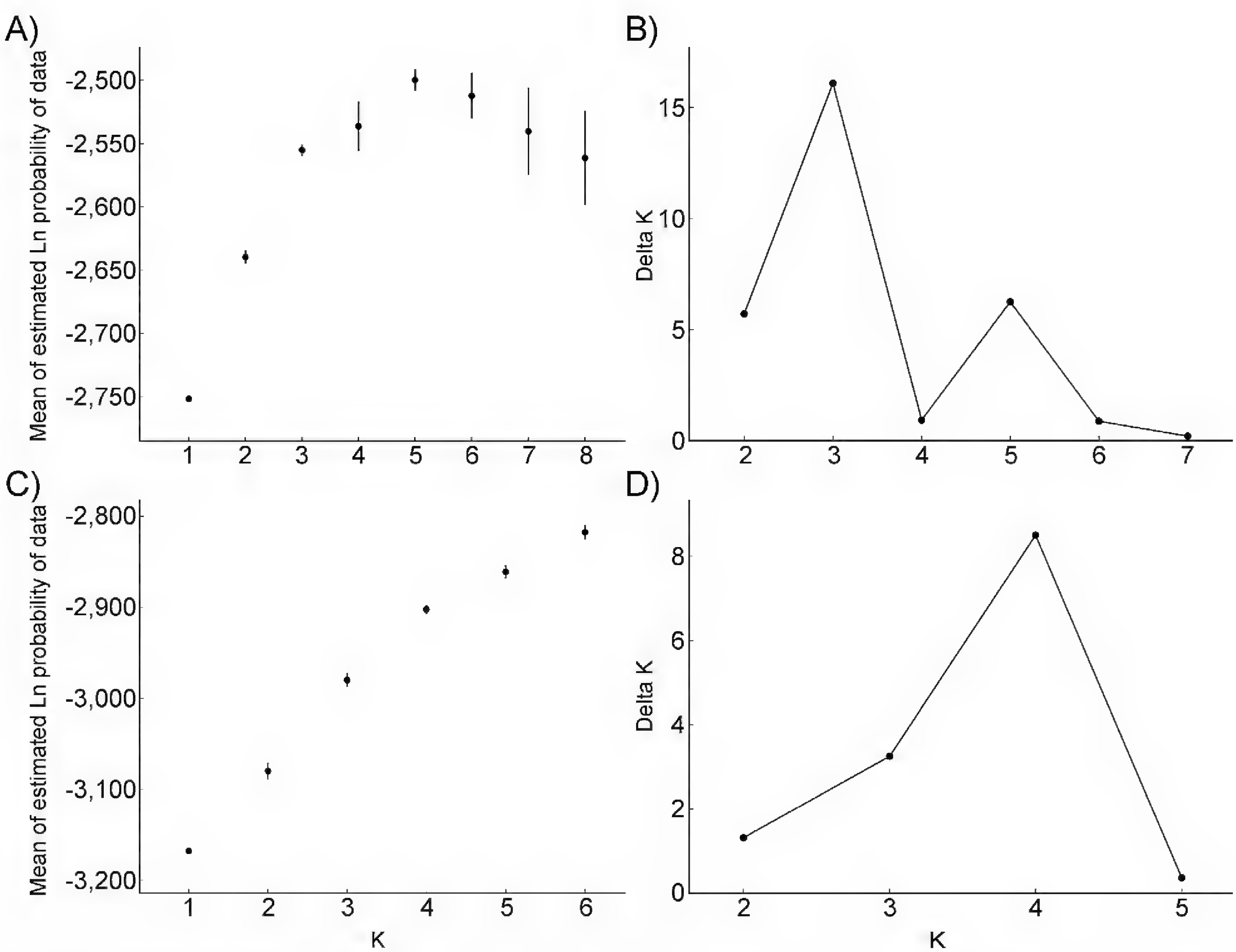
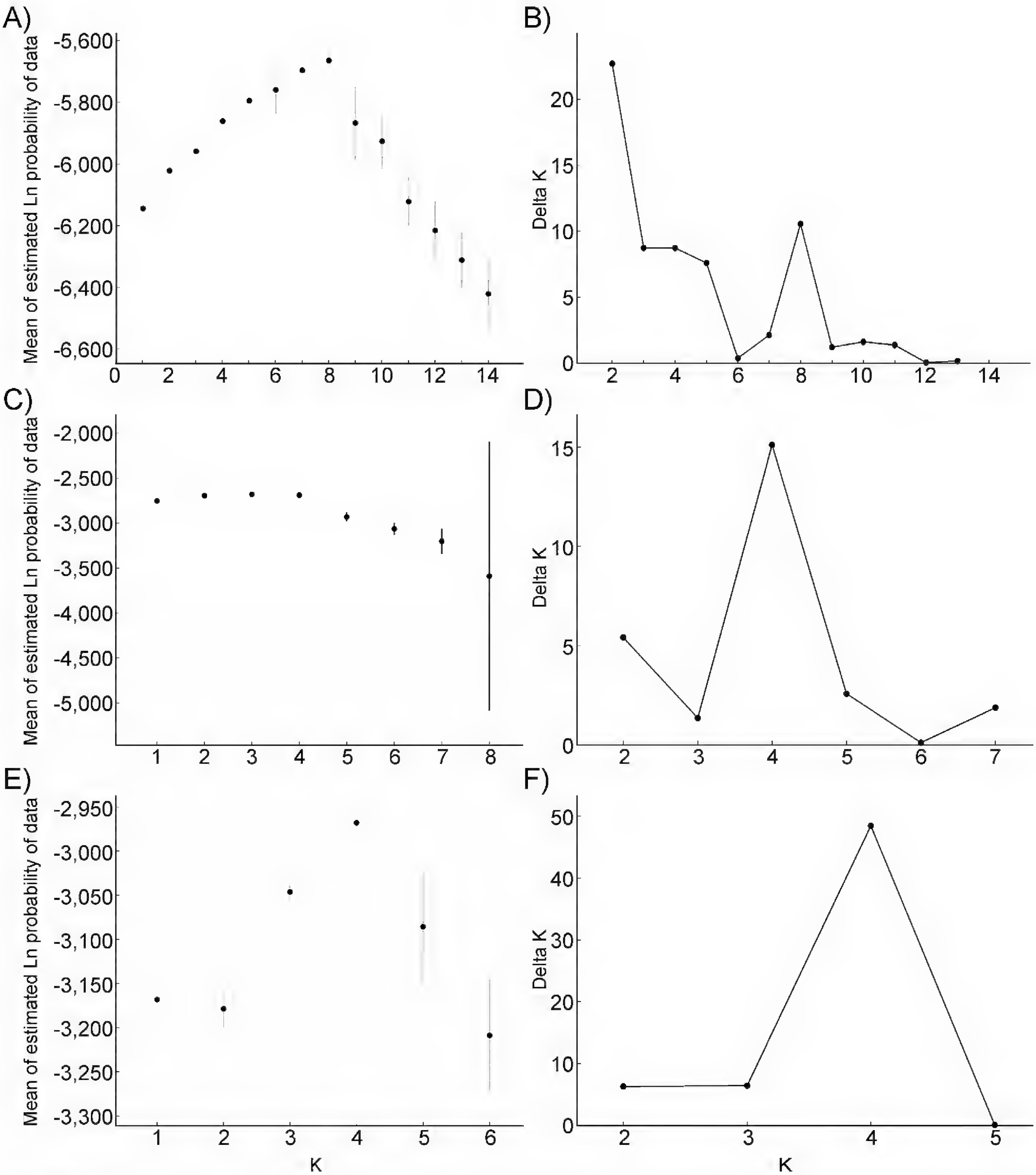
Heike Pröhl discovered her interest in studying frogs in the wild while she studied Biology at the University of Hannover, and while spending a year studying tropical biology at the Universidad de Costa Rica. During that appointment, she benefitted from a wide range of field courses, including herpetology. After sampling field data on Neotropical frog behavior and ecology for her Diploma and Doctoral theses, as well as her Postdoctoral project, she started to work as a Junior Professor at the Veterinary University of Hannover (TiHo) in Germany. Heike is currently an apl. Professor for Zoology and teaches courses related to Zoology, Ecology, and Evolution to biology and veterinary students. Her research focuses on the behavior, ecology, and conservation of Neotropical and European amphibians.



Supplementary Fig. S1. Estimation of the number of *Hyla arborea* populations using the program Structure ver. 2.3.1 (Pritchard et al. 2000) without prior population information; QU, WK, EK, etc. = sample sites, separated by fine black lines. Each individual is represented by a single vertical line broken into *K*-colored segments, with lengths proportional to each of the *K*-inferred clusters. (A) Plot for $K = 2$ in the analysis of the entire data set, (B) plot for $K = 4$, and (C) $K = 4$ for hierarchical analysis on each of the two main clusters.



Supplementary Fig. S2. Mean values of estimated Ln probability of data (LnPD) for each *K* (A, C) and delta *K* (B, D) calculated from Structure runs with Structure Harvester (20 replicates per *K*) in those analyses where prior population information was implemented. (A–B), graphs for hierarchical analysis of the red cluster; (C–D), corresponding graphs for the green cluster (compare to Fig. 3 in the main text).



Supplementary Fig. S3. Mean values of estimated Ln probability of data (LnPD) for each *K* (A, C, E) and delta *K* (B, D, F) without prior population information. (A–B), results for the entire data set. (C–D), graphs for hierarchical analysis of the red cluster. (E–F), corresponding graphs for the green cluster.

Supplementary Table S1. Estimates of evolutionary divergence over cyt *b* sequence pairs between sample sites (*p*-distances).

	QU	WK	EK	KZ	KH	BA	RU	WG	ST	AN	SW	PW
QU	0											
WK	0.001	0										
EK	0.001	0.002	0									
KZ	0.000	0.001	0.001	0								
KH	0.003	0.002	0.004	0.003	0							
BA	0.001	0.001	0.003	0.001	0.002	0						
RU	0.001	0.001	0.002	0.001	0.003	0.002	0					
WG	0.001	0.001	0.002	0.001	0.002	0.001	0.001	0				
ST	0.001	0.001	0.002	0.001	0.002	0.000	0.001	0.001	0			
AN	0.001	0.001	0.002	0.001	0.003	0.001	0.002	0.001	0.001	0		
SW	0.001	0.001	0.002	0.001	0.003	0.001	0.002	0.001	0.001	0.001	0	
PW	0.001	0.001	0.002	0.001	0.002	0.001	0.001	0.001	0.000	0.001	0.001	0

Supplementary Table S2. Geographic distances (km) among sample sites.

	QU	WK	EK	KZ	KO	KH	BH	BA	RU	WG	ST	AN	SW	PW
QU	0	24.89	59.36	118.51	121.07	138.45	138.18	59.60	145.74	186.98	194.94	225.27	214.32	244.29
WK	24.89	0	55.80	121.60	124.18	140.04	140.47	77.42	165.05	189.68	206.53	236.57	221.51	254.05
EK	59.36	55.80	0	66.97	69.52	84.52	85.18	57.94	135.51	134.27	158.58	187.71	168.42	203.12
KZ	118.51	121.60	66.97	0	2.59	20.80	19.80	79.20	107.70	68.55	98.15	125.14	101.84	138.06
KO	121.07	124.18	69.52	2.59	0	18.53	17.33	81.32	107.77	65.97	96.27	123.05	99.39	135.75
KH	138.45	140.04	84.52	20.80	18.53	0	3.94	99.81	118.84	49.76	93.08	117.07	88.33	126.83
BH	138.18	140.47	85.18	19.80	17.33	3.94	0	98.08	115.08	49.22	89.62	114.01	86.17	124.28
BA	59.60	77.42	57.94	79.20	81.32	99.81	98.08	0	87.65	142.67	137.64	167.94	161.85	188.28
RU	145.74	165.05	135.51	107.70	107.77	118.84	115.08	87.65	0	134.01	84.08	108.84	124.69	133.14
WG	186.98	189.68	134.27	68.55	65.97	49.76	49.22	142.67	134.01	0	73.62	86.47	47.60	88.04
ST	194.94	206.53	158.58	98.15	96.27	93.08	89.62	137.64	84.08	73.62	0	30.35	43.49	51.77
AN	225.27	236.57	187.71	125.14	123.05	117.07	114.01	167.94	108.84	86.47	30.35	0	42.06	24.53
SW	214.32	221.51	168.42	101.84	99.39	88.33	86.17	161.85	124.69	47.60	43.49	42.06	0	40.48
PW	244.29	254.05	203.12	138.06	135.75	126.83	124.28	188.28	133.14	88.04	51.77	24.53	40.48	0

Supplementary Table S3. GenBank accession numbers for *Hyla arborea* CytB haplotypes Hy 1 to Hy 11.

Sequence ID	GenBank accession number
BankIt2634361 Seq1	OP690610
BankIt2634361 Seq2	OP690611
BankIt2634361 Seq3	OP690612
BankIt2634361 Seq4	OP690613
BankIt2634361 Seq5	OP690614
BankIt2634361 Seq6	OP690615
BankIt2634361 Seq7	OP690616
BankIt2634361 Seq8	OP690617
BankIt2634361 Seq9	OP690618
BankIt2634361 Seq10	OP690619
BankIt2634361 Seq11	OP690620

Official journal website:
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Amphibian & Reptile Conservation
16(2) [General Section]: 88–103 (e318).

New biological data for two rare reedfrog species, *Hyperolius nimbae* Laurent, 1958, and *H. chlorosteus* (Boulenger, 1915) (Anura: Hyperoliidae)

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***Abstract.*—Our recent surveys have generated new biological data on *Hyperolius nimbae* and *H. chlorosteus*, two little-known West African reedfrog species of conservation concern. During fieldwork at the eastern foothills of the Ivorian part of the Nimba Mountains, *H. nimbae* and *H. chlorosteus* individuals were found by acoustic and visual encounter surveys. In addition, various natural history data were recorded, including clutch size and egg-deposition sites. *Hyperolius nimbae* males were found at the edges of a permanent swamp. The area was dominated by cocoa and coffee plantations, and used in small-scale subsistence farming, i.e., growing plantains, cassava, and rice. A new locality is reported here for the species, but our surveys failed to confirm its presence at some previously known sites. The entire range of the species is now confined to a small, non-protected, human-impacted area. Under these conditions, this species is facing high extinction risk. *Hyperolius chlorosteus* was found in a patch of dense, broadleaf and evergreen primary forest at a mid-elevation along a torrent stream, and in a degraded lowland forest edging a large stream. The habitats of both species are suffering from forest degradation and deforestation along streams, so we urgently recommend the strict protection of the habitats of both species. Given these concerns, we suggest that the IUCN threat status of *H. nimbae* should be updated to Critically Endangered. Considering the large range of *H. chlorosteus*, the current IUCN categorization of this species as Least Concern seems to be correct. However, based on the fact that in Ivory Coast it only occurs in the westernmost parts of the country, several of the few known national populations have been lost, and the remaining forest habitats are declining, so we feel that *H. chlorosteus* should be regarded as Endangered nationally.**

Keywords. Biodiversity hotspot, endemic, habitat protection, Mount Nimba Reedfrog, Threatened species, Upper Guinean forest area

Citation: Gongomin BA-I, Kouamé NG, Agoh KL, Kanga KP, Rödel M-O. 2022. New biological data for two rare reedfrog species, *Hyperolius nimbae* Laurent, 1958, and *H. chlorosteus* (Boulenger, 1915) (Anura: Hyperoliidae). *Amphibian & Reptile Conservation* 16(2) [General Section]: 88–103 (e318).

Accepted: 23 August 2022; **Published:** 24 October 2022

Introduction

Ivorian montane areas, such as Mount Péko, Mount Sangbé, and Mount Nimba, are small in extent but comprise a high diversity of amphibian species (e.g., Rödel 2003; Rödel and Ernst 2003; Kanga et al. 2021). Mount Nimba, in particular, hosts the richest amphibian fauna of West Africa including various rare and endemic species (Kanga et al. 2021; Rödel et al. 2021). For instance, this mountain is the only known region where the matrotrophic Nimba Toad, *Nimbaphrynoides occidentalis* (Angel, 1943), and the Mount Nimba Reedfrog, *Hyperolius nimbae* Laurent, 1958, are found. The biology of *N. occidentalis* has been investigated in detail (Lamotte 1959; Lamotte and Sanchez-Lamotte 1999; Xavier 2009; Sandberger et al. 2010; Sandberger-Loua et al. 2017, 2018), and this toad is considered to be the flagship species for the conservation of the Nimba mountains (Hillers et al. 2008a; Sandberger-Loua et al. 2016).

Much less attention has been directed toward various other little-known amphibian species which are, nevertheless, of high conservation concern in Ivory Coast. These include, two notable reedfrogs, the Mount Nimba Reedfrog *Hyperolius nimbae* and the Large Green Reedfrog *H. chlorosteus* (Boulenger, 1915), for which

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we know very little concerning their life histories.

Hyperolius nimbae is currently classified as Endangered on *The IUCN Red List of Threatened Species* (IUCN 2021). It is endemic to the lowlands of the eastern slopes of the Ivorian part of Mounts Nimba. After Schiøtz (1967) last collected this frog on 28 July 1963, the species was only recently rediscovered by Kouamé et al. (2016). This species is rare throughout its limited range in some swamp forests near Danané (Schiøtz 1967; Kouamé et al. 2016; Kanga et al. 2021). By contrast, *H. chlorosteus* inhabits rainforests in Sierra Leone, Guinea, Liberia, and western Ivory Coast (Rödel et al. 2004; Channing and Rödel 2019) and is categorized as Least Concern on the IUCN Red List (IUCN 2021). Despite a broad distribution, *H. chlorosteus* is confined to the edges of rivers in primary lowland forests (Schiøtz 1967; Rödel and Glos 2019), and thus must be regarded as threatened in Ivory Coast due to the decline of those habitats. A previously known population in Lakota (south-central Ivory Coast; Schiøtz 1967) no longer exists, and more may have been lost due to deforestation. For instance, Ivorian records of *H. chlorosteus* have been published from the classified forests (managed forests) of Cavally and Haute Dodo (Rödel and Branch 2002), and the national parks of Mount Sangbé (Rödel 2003), Mount Péko (Rödel and Ernst 2003), and Taï (e.g., Ernst and Rödel 2008; Kpan et al. 2021), as well as from Mount Nimba (Kanga et al. 2021), which are all situated in the south-western part of the country. However, during a decade of conflict, the gallery forests in Mount Péko as well as both classified forests have been destroyed (NG Kouamé, pers. obs.). These losses restrict the remaining known Ivorian range of *H. chlorosteus* to the southern part of Mount Sangbé, the lowland forests of Mount Nimba, and the Taï National Park.

The aim of this study was to search for the persisting populations of *H. nimbae* and *H. chlorosteus* at Mount Nimba, and to collect additional data on the morphology, call characteristics, breeding sites, and potential threats for these poorly-known species.

Material and Methods

Study site. Fieldwork was conducted in the Mount Nimba Integrated Nature Reserve (MNINR: 07°25'–07°45'N, 008°20'–008°35'W; Fig. 1) during both the rainy and dry seasons, and was carried out on 84 days between 2 August 2019 and 8 July 2020. The MNINR covers 5,000 ha of various habitats ranging from altered and former forests in the lowlands, through dense, broadleaf and evergreen forests stretching from the lower to mid-elevations, and montane grasslands at the highest elevations (Lamotte et al. 2003a,b; Lauginie 2007). Mean annual temperatures vary from 22–27 °C on the mountain bases, and 16–21 °C on the mountain ridge. The rainy season extends from eight to nine months and is only interrupted by a short dry season from November/December to February/March. The precipitation is highest on the mountain top, where it may reach up to 3,500 mm. During the dry season, the humidity is usually below 30%, but exceeds 80% in the rainy season (Lauginie 2007). The dry season is characterized by a warm, dry, and dusty wind known as Harmattan. For a detailed description of MNINR's amphibian fauna see Kanga et al. (2021).

Sampling. As previous research has shown that these two reedfrog species are only active at night (Kanga et al. 2021), searches took place from 1800–2200 h GMT. All searches were conducted by three people, totalling a search-effort of 1,008 person-hours. Search techniques focused on visual scanning of the terrain, supplemented by acoustic surveying to find the males, and examination of potential calling and breeding sites. Particular attention was given to searching the vegetation around and/or along forest streams and swamps. We investigated the area seven times per month and counted only individuals that were captured.

Hyperolius nimbae was found at one site at Yéalé, while *H. chlorosteus* was collected at one site at MNINR and another site at Yéalé. We visited each site 56 times in the rainy season and 28 times in the dry season (Table 1; Appendices 1 and 2). Frogs were photographed, measured, and sexed. To avoid re-counting frogs, individuals that were not collected were marked as vouchers by toe clipping following the recommendations of Grafe et al. (2011), and released at their respective sites of capture. Areas close to four villages (Dagbonpleu, Danipleu, Kouan-Houlé, and Zéalé), within the formerly known range of *H. nimbae,* were re-investigated seven times. These visits were in the rainy season, which is the presumed reproductive period of the species. We recorded potential threats to *H. nimbae* and *H. chlorosteus*, defined here as any anthropogenic activity that may negatively impact the two species and/or their habitats.

Although the panzootic chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*) seems to be absent from West Africa, west of the Dahomey Gap (Penner et al. 2013), newly sterilized equipment was always used at each site. Geographical coordinates were recorded with a GPS (datum: WGS84). A few vouchers were euthanized in a 1,1,1-trichloro-2-methyl-2-propanol hemihydrate (MS222) solution and thereafter preserved in 80% ethanol. These frogs are deposited in the research collection of NGK at the Université Jean Lorougnon Guédé, Daloa, Ivory Coast, and will serve as the bases of a national reference collection and for research and teaching purposes.

Morphological characteristics and advertisement calls. Measurements of morphological features (in mm) were taken by one person (BAIG) with a dial calliper (accuracy ± 0.1 mm), and are given as means ($\bar{X}$) with standard deviations (SD). They comprise: snout-urostyle length, head width and length both at the level of jaw

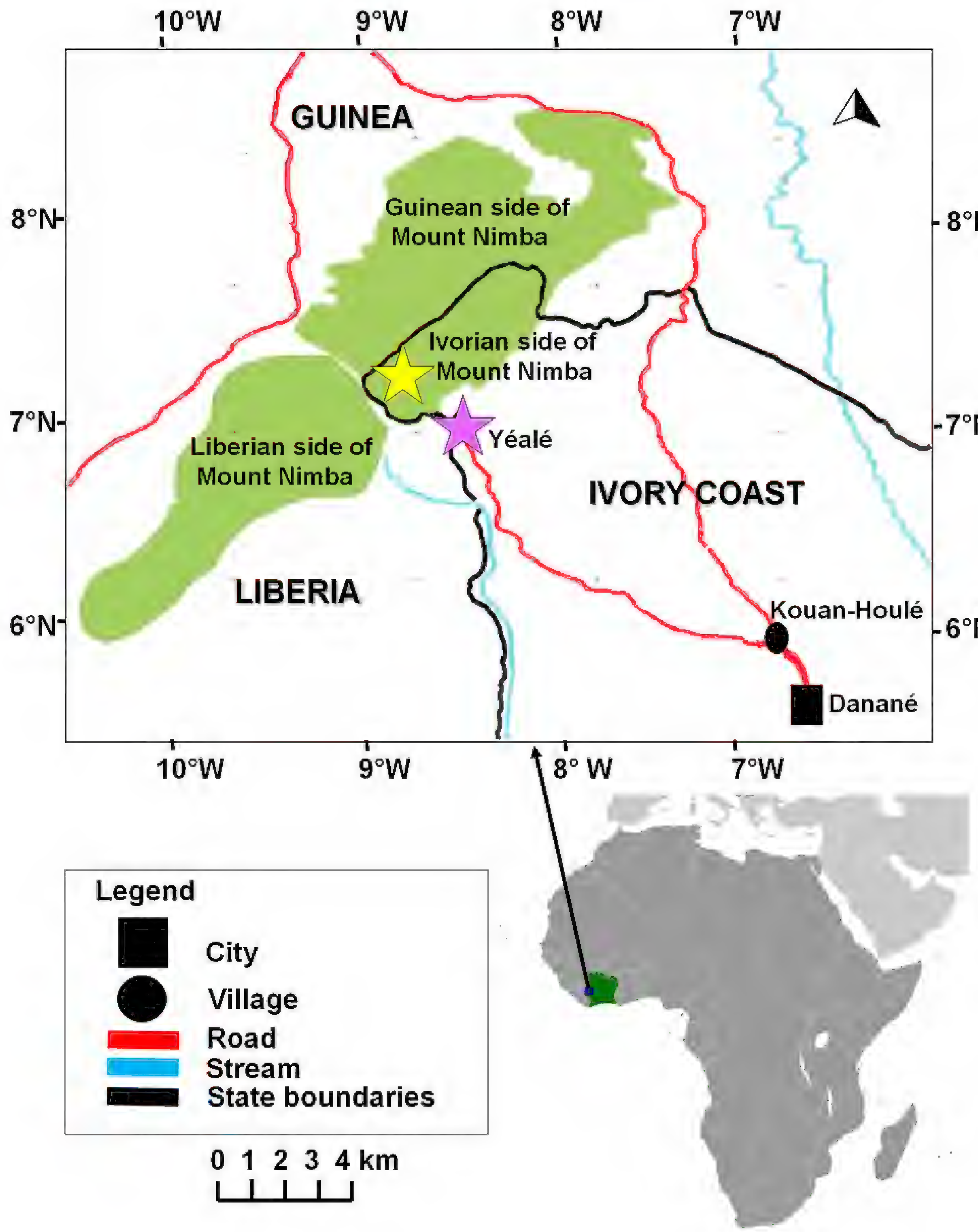

Fig. 1. Geographical location of the Mount Nimba Integrated Nature Reserve within the westernmost extension of Ivory Coast at the border crossing point with Guinea and Liberia. The altered forest area where *Hyperolius nimbae* and *H. chlorosteus* were found at Yéalé is represented by a purple star; the habitats of *H. chlorosteus* ranged from dense, broadleaf and evergreen forests from lower to mid-elevations (yellow star). The inset figure indicates the location of Ivory Coast (green patch) on the African continent.

articulation, interorbital space, distance between eye and nostril, distance from nostril to tip of snout, eye diameter, internarial distance, tympanum diameter, crus length, thigh length, and foot length including the tarsus and the longest toe.

Other characters recorded included color pattern variation following the definitions by Schiøtz (1967) and Channing and Rödel (2019). To ensure that clutches of *H. nimbae* and *H. chlorosteus* could not be confused with those of other sympatric reedfrogs, couples were collected and kept separately in a plastic terrarium (25 × 15 cm, 16 cm depth) with water (8.5 cm) and submerged and floating vegetation until eggs were laid. Egg numbers and diameters (accuracy ± 0.1 mm) were determined for each clutch. For comparison, further *H. chlorosteus* clutch data collected between 1999 and 2001 in Taï National Park by MOR are also reported here.

Hyperolius nimbae was not included in a phylogeny of the genus (Portik et al. 2019), but is assumed to be a member of the *H. viridiflavus* complex (Schiøtz 1999; Channing 2022). Very recently, this was confirmed by genetic data, and it was shown to be the sister species to

Table 1. Numbers of daily searches for *Hyperolius nimbae* and *H. chlorosteus*, during the 84-night period from 2 August 2019 to 8 July 2020, in Mount Nimba Integrated Nature Reserve and Yéalé.

	Hyperolius nimbae	***Hyperolius chlorosteus***	
Site of capture	Yéalé (07°31.928'N, 008°25.401'W; 425 m asl)	MNINR (07°34.652'N, 008°24.966'W; 716 m asl)	Yéalé (07°31.932'N, 008°25.508'W; 387 m asl)
Number of visits during the rainy season	56	56	56
Number of visits during the dry season	28	28	28

the Central African *H. tuberculatus* (Kouamé et al. 2022). Nine sequential advertisement calls were collected from one male, in order to compare these data with those presented by Schiøtz (1967). Five advertisement calls were also recorded from a *H. chlorosteus* male.

All calls were recorded with a Huawei recorder (44.1 kHz sample ratio, 16 bits of resolution, FFT length = 256) and analyzed with the software Soundruler 0.9.6 (Gridi-Papp 2007; Köhler et al. 2017; Emmrich et al. 2020). For each advertisement call, the following measurements were recorded: call duration (s), dominant frequency (Hz), fundamental frequency (Hz), minimum frequency (Hz), maximum frequency (Hz), duration intervals between calls (s), duration intervals between notes (s), and overall frequency bandwidth (Hz).

Results

Observations on *H. nimbae*

Habitat, population size, and activity of *H. nimbae*. The Mount Nimba Reedfrog was found only in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl) at the periphery of MNINR. Our efforts to confirm the species around village forests at Dagbonpleu, Danipleu, Kouan-Houlé, and Zéalé were unsuccessful. The forest areas formerly at these sites were destroyed and replaced by roads and new settlements. At Yéalé, the habitat comprised altered forest bordered by patches of bamboo, intact forests, degraded forests with large clearings, and thick grassy and shrubby vegetation around the settlement. Large parts of the village's surroundings were dominated by small-scale subsistence farming, mainly plantings of corn, cassava, plantains, cocoa, and coffee, as well as rice in swamps. During the entire study, the vegetation around swamps was checked at seven sites without detecting any sign of *H. nimbae*'s presence.

Specimens of *H. nimbae* were found only in a mixed cocoa and coffee plantation (including plantains) edging a large and deep pond (greater than 100 x 70 m; Fig. 2), where males started calling at dusk, usually around 1810 h GMT. Calling males were active in each month of our study and congregated in large choruses, particularly during the rainy season. Calling activity never stopped, but was low during the dry season, as indicated by the much lower numbers of frogs caught during that time (Fig. 3). The calling males were mostly well concealed, perching between thick branches and leaves of cocoa and coffee trees at ~1.80–2.10 m above the ground. Througout the study, a total of 305 frogs were captured (Fig. 3; Appendix 1). They comprised 277 individuals, including one couple, caught in the rainy season and 28 males caught in the dry season. Generally, additional calling males were inaccessible, calling from high up in tall trees close to the deep pond.

Sympatric amphibian species in Yéalé were the White-lipped Frogs *Amnirana* sp. "albolabris west", *Afrixalus dorsalis*, *A. fulvovittatus*, *Hyperolius concolor*, *H. fusciventris fusciventris*, *H. picturatus*, *Phrynobatrachus gutturosus*, and *P. latifrons*, thus representing a typical composition of a farmbush anuran community (Schiøtz 1967).

Morphology of *H. nimbae*. We retained 13 males and one female *H. nimbae* as vouchers. Snout-urostyle lengths of the voucher males ranged from 28.8–35.0 mm (32.3 ± 1.8 mm), thus slightly exceeding the known range of *H. nimbae* (Schiøtz 1967). The head was slightly longer (12.0 ± 1.1 mm; range: 10.0–13.5 mm) than broad (10.8 ± 0.8 mm; range: 9.9–12.5 mm); interorbital space ranged from 5.0–7.5 mm (6.4 ± 0.7 mm); the distance between eye and nostril (2.1 ± 0.3 mm; range: 2.0–3.0 mm) approximated the distance from nostril to tip of snout (2.2 ± 0.3; range: 1.5–2.0 mm); eye diameter (4.6 ± 0.4 mm; range: 4.0–5.1 mm) was larger than internarial space (3.2 ± 0.3 mm; range: 3.0–4.0 mm) and tympanum diameter (2.3 ± 0.3 mm; range: 2.0–3.0 mm); crus length (16.5 ± 1.0 mm; range: 15.1–18.9 mm) slightly exceeded thigh length (15.0 ± 0.8 mm; range: 13.5–16.1 mm); and foot length including the longest toe ranged from 21.0–26.9 mm (23.1 ± 1.6 mm).

The female measured 34.0 mm SUL (Fig. 4A). Its head was slightly longer (14.0 mm) than broad (12.1 mm); the interorbital space reached 8.0 mm; the distance between eye and nostril (3.4 mm) was longer than the distance from nostril to tip of snout (1.8 mm); eye diameter (5.0 mm) was larger than internarial space (3.0 mm) and tympanum diameter (2.9 mm); crus length (18.0 mm) slightly exceeded thigh length (17.1 mm); and foot length including the tarsus and the longest toe reached 24.5 mm.

Mount Nimba reedfrogs have a brief and truncated

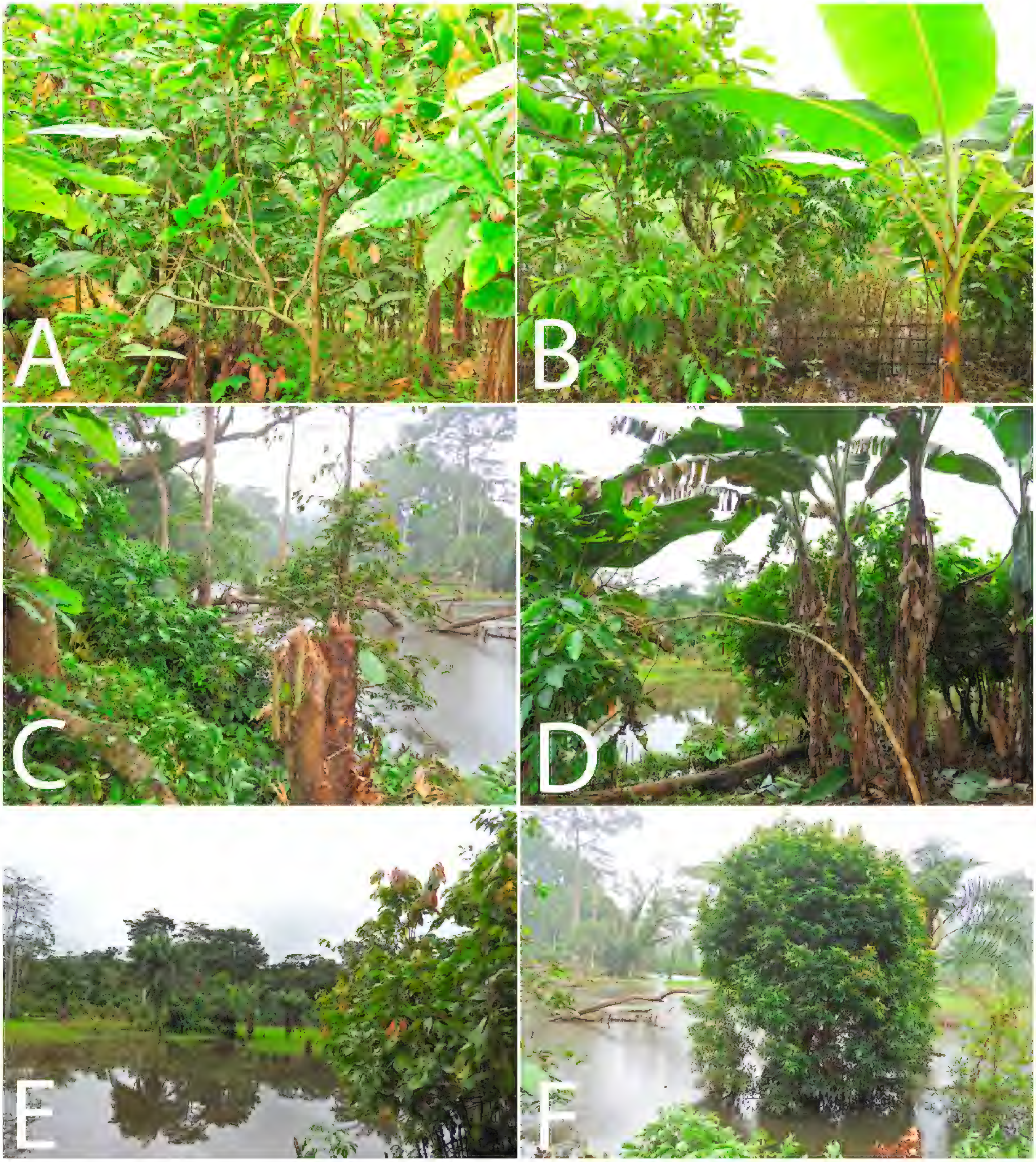

Fig. 2. Habitats of *Hyperolius nimbae* at the foothills of the Ivorian part of the Nimba Mountains. In Yéalé, the species was found in heavily degraded habitats at the edge of large swamps.

snout and rough to warty dorsal skin with a varied color pattern. The basic dorsal pattern varied from silver-grey to chocolate brown. The dark pattern on the back varied in intensity, but the general pattern was always similar and recognizable (Fig. 4). The female coloration was within the variation of the males (Fig. 4), but the discs on toes and fingers were more reddish than in most males (Fig. 4A). Likewise, the ventral color differed slightly between individuals, but the female was not different from the males (Fig. 5). However, instead of a dark vocal sac and yellowish gular gland, the female had a white throat, with the edges beset by orange and black speckles. The armpits and inner parts of limbs including webbing were blood red (Fig. 5C). Some males had similarly reddish skin parts (Fig. 5A), areas which are used for water uptake, see Rödel (2000), whereas others had blue-grey skin instead (Fig. 5B).

Reproduction of *H. nimbae*. At Yéalé, a couple of *H. nimbae* in amplexus was captured on a *Raphia* Palm in

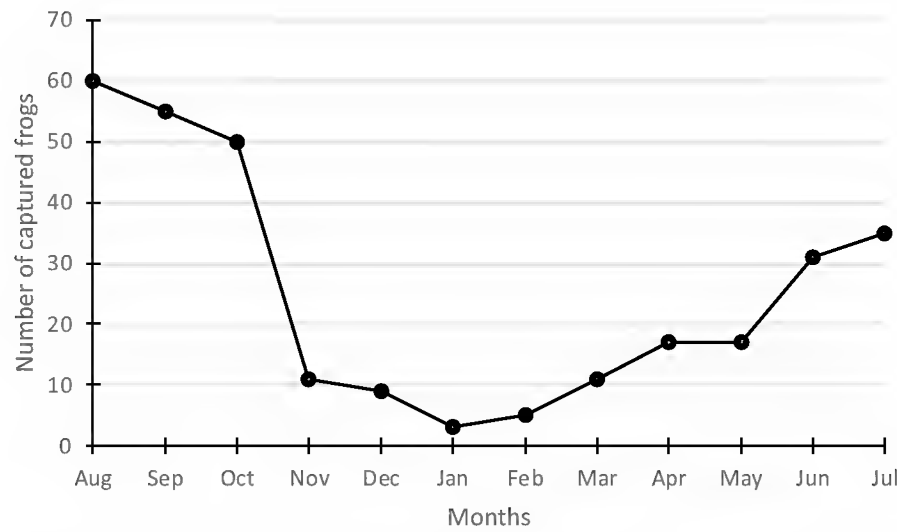

Fig. 3. Number of *Hyperolius nimbae* individuals recorded from 2 August 2019 to 8 July 2020 at Yéalé.

deeper water (> 1 m). The couple was placed into a terrarium, and the following morning, 227 eggs were found attached to a leaf above the water surface. The eggs had a dark and light green pole that was surrounded by a thin transparent jelly (Fig. 5D). Egg diameter varied from 1.6–2.5 mm, with a mean value of 1.99 mm (SD: ± 0.18 mm).

Vocalization of *H. nimbae*. The acoustic properties of nine advertisement calls of one *H. nimbae* male were analyzed (Fig. 6). *Hyperolius nimbae* call in a long, fast series of pulse groups (notes), thus confirming the call descriptions provided by Schiøtz (1967). The call duration averaged 2.77 ± 0.56 s (range: 1.89–3.25 s). The duration intervals between calls averaged 0.44 ± 0.23 s (range: 0.22–0.87 s, N = 8). Intervals between notes within each call were 0.15 ± 0.03 s (range: 0.09–3.48 s, N = 131). The mean fundamental frequency was 1,359.37 Hz (N = 9), while the dominant frequency reached 2,718.75 Hz (N = 9). The maximum frequency intensity was at 2,906.25 Hz (N = 9), and the minimum frequency intensity averaged 2,718.75 Hz (N = 9).

Threats to *H. nimbae*. We failed to confirm the species presence at all sites where we had recorded it only a few years before (see above). In addition, we observed various signs of habitat degradation in the habitats of *H. nimbae* at Yéalé. Aside from the close proximity to a human settlement, the frogs' habitats were dominated by cocoa and coffee plants, and used for small-scale subsistence farming, i.e., plantains and cassava. Large parts of the breeding area of *H. nimbae* were used to establish rice paddies. Bamboo patches were steadily harvested by the local human population as construction materials. The rainforest edges were impacted by logging (Fig. 2).

Observations on *H. chlorosteus*

Habitat, population size, and activity of *H. chlorosteus*. Specimens of *H. chlorosteus* were found in MNINR in a patch of dense, broadleaf and evergreen primary forest at a mid-elevation along a torrent stream (07°34.652'N, 008°24.966'W; 716 m asl; Fig. 7A), as well as in a degraded forest edging a large stream at Yéalé village (07°31.932'N, 008°25.508'W; 387 m asl; Fig. 7B). From April–November, the rainy season, a total of 341 *H. chlorosteus* were captured in the two sites, always at night along the streams (Fig. 8; Appendix 2). In the dry season, from December to March, no signs of the species' presence were observed. Males started calling at around 1800 h GMT, most often after heavy rainfall. In a patch of primary forest, 327 calling males perched on leaves and branches of small shrubs at ~1.5–2.0 m height above the ground (e.g., Fig. 7C) were captured. The other recorded males were heard calling from very high up in tall trees along the forest stream. A few calling males (N = 11) were also found in a degraded forest, edging a large stream at Yéalé village (07°31.932'N, 008°25.508'W; 387 m asl; Fig. 7B). There, they called on shrubs, with the calling sites ranging from 1.80 m above the ground to much higher. Sympatric frogs were *Leptopelis macrotis*, *Hyperolius picturatus*, and White-lipped Frogs *Amnirana* sp. "albolabris west."

Morphology of *H. chlorosteus*. The snout-urostyle lengths of 15 males, retained as vouchers, ranged from 31.5–35.0 mm (33.8 ± 1.3 mm), thus occurring within the known range of *H. chlorosteus* (Schiøtz 1967). The head was slightly longer (12.0 ± 0.1 mm; range: 12.0–12.2 mm) than broad (11.5 ± 0.7 mm; range: 10.5–13.0 mm); the interorbital space ranged from 5.9–7.2 mm (6.5 ± 0.4 mm); the distance between eye and nostril (3.0 ± 0.2 mm; range: 2.5–3.5 mm) was approximately twice the distance from nostril to tip of snout (1.4 ± 0.6; range: 0.6–2.4 mm); the eye diamter (5.1 ± 0.3 mm; range: 4.4–5.5 mm) was larger than internarial space (2.6 ± 0.4 mm; range: 2.1–3.0 mm) and tympanum diameter (2.8 ± 0.2 mm; range: 2.2–3.0 mm); the crus length (17.0 ± 0.7 mm; range: 15.4–18.1 mm) slightly exceeded the thigh length (15.9 ± 0.8 mm; range: 14.9–16.9 mm); and foot length including the longest toe ranged from 21.5–23.5 mm (22.2 ± 0.8 mm).

Two females measured 36.8 and 37.5 mm in SUL. As in the males, their heads were slightly longer (13.5 mm) than broad (13.2 mm); interorbital spaces were 7.0 and 7.2 mm; the distance between eye and nostril was longer (3.3 ± 0.3 mm; range: 3.1–3.5 mm) than the distance from nostril to tip of snout (1.9 ± 0.1 mm; range: 1.9–2.0 mm); the eye diamter (5.0 ± 0.1 mm; range: 5.0–5.1 mm) exceeded the internarial space (2.9 ± 0.1 mm; range: 2.9–3.0 mm) and tympanum diameter (2.9 ± 0.1 mm; range: 2.8–3.0 mm); the crus length (17.7 ± 0.3 mm; range: 17.5–17.9 mm) slightly exceeded thigh length (16.9 ± 1.5 mm; range: 15.9–18.0 mm); and foot length including the tarsus and longest toe ranged from 23.5–23.8 mm (23.6 ± 0.2 mm).

The color pattern of *H. chlorosteus* showed some variations (see Figs. 7 and 9), however, all were within the range known for the species (compare Schiøtz 1967; Rödel 2003; Channing and Rödel 2019).

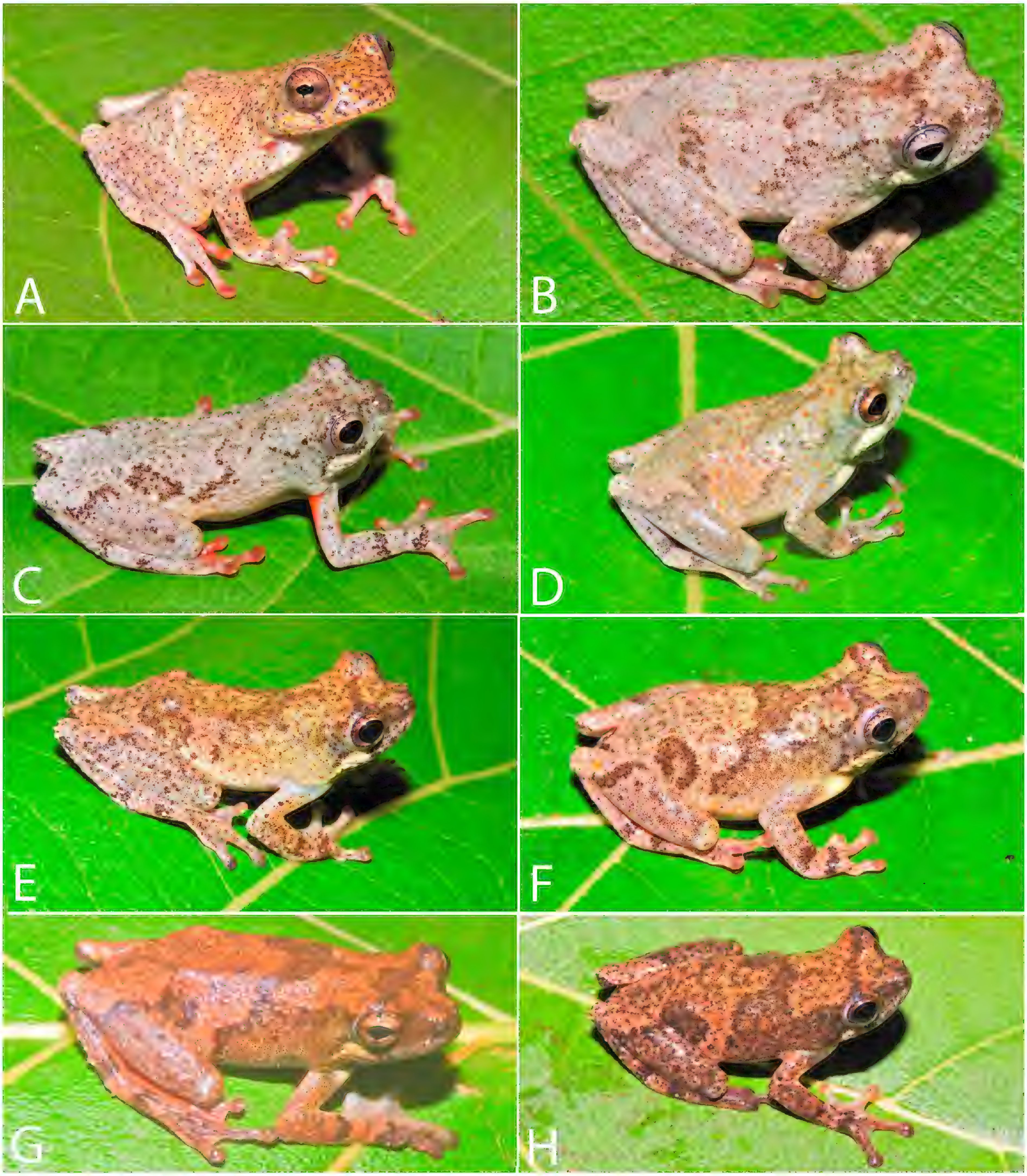

Fig. 4. Dorsolateral views of the *Hyperolius nimbae* female **(A)** and males **(B–H)** from Yéalé, western Ivory Coast. Note the variation in coloration.

Reproduction of *H. chlorosteus*. One female perched on a broad leaf of a shrub overhanging a forest stream, at ~1.5 m height, was captured. Eggs were visible through its ventral skin (Figs. 7D and 9F). An amplectant couple was seen sitting on low vegetation in this site (Fig. 7E). This couple was placed in a terrarium and a clutch of 62 eggs was present the next morning. The eggs were attached to the glass above the water. They had beige and dark poles surrounded by a thin transparent capsule (Fig. 7F). Egg diameters varied from 2.0–2.5 mm, mean 2.2 mm (SD: ± 0.25 mm). The jelly of *H. chlorosteus* eggs is slightly opaque. Six additional *H. chlorosteus* clutches observed in Taï National Park, south-west of Ivory Coast, ranged from 54–122 eggs (86.2 ± 28.8 eggs; Table 2).

Vocalization of *H. chlorosteus*. Five advertisement calls were recorded from one male (Fig. 10). The calls were repeated 2–7 times (Fig. 10B). The acoustic impression

Table 2. Data for *Hyperolius chlorosteus* clutches from Taï National Park, Ivory Coast.

Clutch number	Date	Number of eggs	Location of clutch	Remarks
1	14 March 1999	54	On tree above stream	None
2	16 March 1999	120	Attached to leaf, 2 m above stream	Clutch looks like a blackberry
3	16 March 1999	85	Attached to leaf, 2 m above stream	None
4	16 March 1999	65	1.4 m above stream	None
5	23 March 1999	122	Not recorded	Egg size 3–6 mm, nucleus 1.9–2 mm; clutch looks like a blackberry
6	4 February 1999	71	Clutch on stone covered with mosses above water	Egg size 3–6 mm, nucleus 2.2 mm; looks like a blackberry

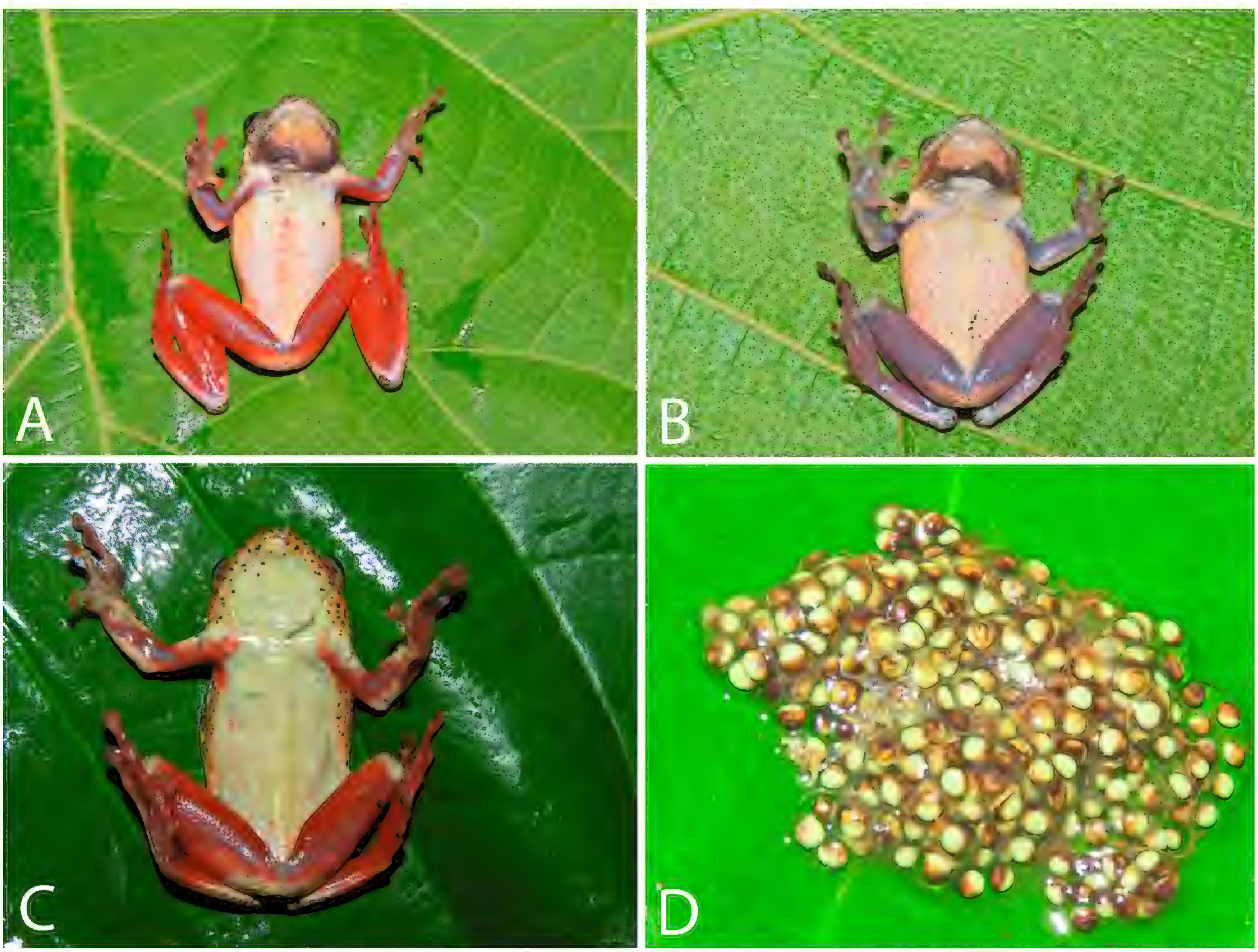

Fig. 5. Ventral views of *Hyperolius nimbae* males **(A** and **B)** and female **(C)** adults, and the eggs **(D)** from Yéalé, western Ivory Coast.

of the call is a low-pitched, far ranging metallic click with a mean duration of 0.87 ± 0.34 s (range: 0.51–1.41 s). The duration intervals between calls averaged 2.90 ± 1.27 s (range: 1.36–4.0 s, $N = 4$). The mean fundamental frequency was 1,303.12 ± 83.85 Hz (range: 1,265.62–1,453.12 Hz, $N = 5$), while the dominant frequency reached 2,606.3 ± 167.70 Hz (range: 2,531.25–2,906.25 Hz, $N = 5$). The maximum frequency intensity was at 2,643.75 ± 167.70 Hz (range: 2,531.25–2,906.25 Hz, $N = 5$), and the minimum frequency intensity averaged at 2,531.25 ± 229.64 Hz (range: 2,343.75–2,906.25 Hz, $N = 5$).

Threats to *H. chlorosteus*. Major threats to *H.*

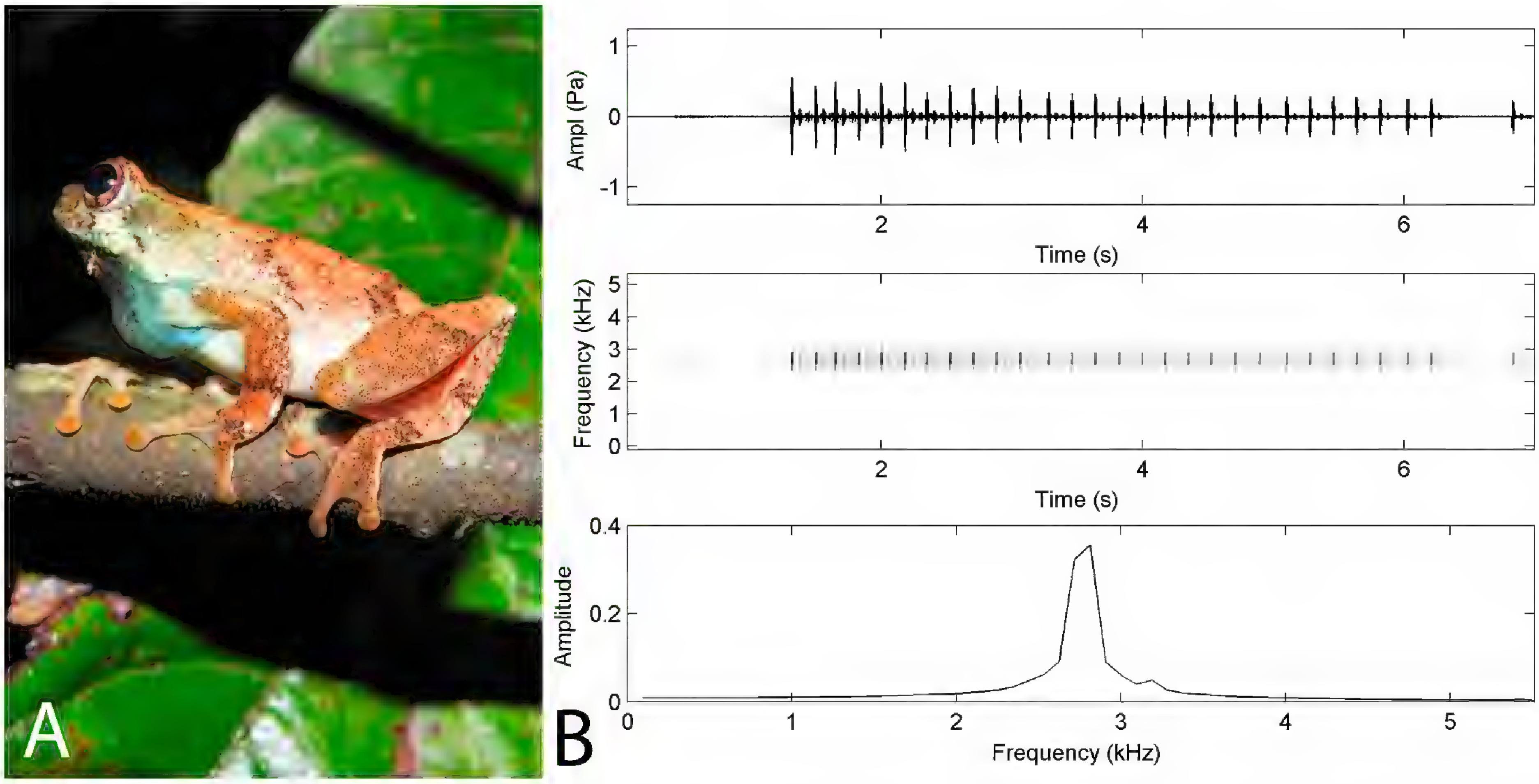

Fig. 6. (A) *Hyperolius nimbae* usually calls perched between branches and leaves of trees. **(B)** Waveform (above), spectogram (center), and powerspectrogram (below) of the advertisement calls of a *H. nimbae* male from Yéalé, western Ivory Coast.

chlorosteus were observed at Yéalé, where some forest pockets along streams had been cleared and converted to cocoa and coffee plantations, as well as rice cultivation.

Discussion

This study gathered new data on the biology and distribution of two rare reedfrog species, *Hyperolius nimbae* and *H. chlorosteus*, living in different forest habitats in the western Upper Guinea forest zone (Channing and Rödel 2019). *Hyperolius nimbae* has been documented only from a few individuals and populations on the Ivorian part of the Nimba Mountains (Schiøtz 1967; Kouamé et al. 2016; Kanga et al. 2021), and little was known about its phenotypic variation, biology, and habitat requirements prior to this study. A recent study based on 16S rRNA sequences of members of the *H. viridiflavus* clade revealed that *H. nimbae* is a member of the *H. viridiflavus* clade and sister species to the Central African *H. tuberculatus* (Kouamé et al. 2022).

At Yéalé, a relatively large population of *H. nimbae* was found in patches of heavily degraded forest area, partly neighboring human settlements. This habitat fit well with the earlier habitat description, i.e., from the villages at Dagbonpleu, Danipleu, Kouan-Houlé, and Zéalé (Kouamé et al. 2016). However, an alarming result of this study is that due to ongoing development of the area, all formerly known sites have been destroyed, restricting the currently known range of *H. nimbae* to Yéalé alone.

Our morphological assessments of a larger number of individuals confirmed former descriptions, but slightly increased our knowledge about color variability (Schiøtz 1967; Kouamé et al. 2016; Figs. 3 and 4). *Hyperolius nimbae* apparently is another reedfrog species that lacks sex specific color dimorphism (compare Schiøtz 1967; Veith et al. 2009; Portik et al. 2019). The new data herein also confirms previous descriptions of the advertisement calls of *H. nimbae* (Schiøtz 1967). In contrast to most other *Hyperolius* (Schiøtz 1967, 1999), *H. nimbae* males always produce a succession of continuous clicks and thus much longer calls.

Most *Hyperolius* species are "prolonged breeders" (Schiøtz 1967, 1999; Lötters et al. 2004; Rödel et al. 2006; Kouamé et al. 2015). *Hyperolius nimbae* is no exception to that rule, with males calling during all months of the rainy season, usually at the edges of large and permanent water bodies. We documented the first known clutch for this species (Fig. 5D). The eggs were attached to a leaf above the water surface, a feature which is common to forest species within *Hyperolius*. Savannah dwelling *Hyperolius* species deposit eggs under water, most likely as a response to the higher desiccation risk (Rödel 2000). We take the egg deposition above water as a further hint that this species depends on forest, at least to some extent.

It remains a mystery why *H. nimbae* apparently tolerates degraded forests but only occurs in the Ivorian foothills of Mount Nimba, as comparable habitats are available beyond its range (Schiøtz 1967). Most likely this species was trapped at these sites when the Nimba mountains were surrounded by savannah during drier periods, representing a refugium for the survival of forest species during unfavorable Pleistocene periods (Maley 1996).

The new *Hyperolius chlorosteus* data reported herein confirmed previous descriptions of the morphology and advertisement call (Schiøtz 1967, 1999; Channing and Rödel 2019). This species is morphologically similar to

Fig. 7. (A–B) Typical forest streams in the Mount Nimba Integrated Nature Reserve where *Hyperolius chlorosteus* breeds. A calling male **(C)**, a female **(D)**, a couple in amplexus **(E)**, and their clutch **(F)** which was deposited on a leaf above a forest stream.

H. laurenti (from the eastern parts of the Upper Guinea forest zone; Schiøtz 1967, 1999; Channing and Rödel 2019), with which it also shares habitat requirements, i.e., perching on branches above small to medium-sized streams in primary or only slightly degraded forests, often at considerable height (Rödel et al. 2005; Kouamé et al. 2014). The breeding period of *H. chlorosteus* is confined to the rainy season, and clutches are attached at various heights on leaves, branches, and stones above flowing water.

The habitat characteristics of *H. chlorosteus* encountered in MNINR were similar to those reported from previous sites, i.e., dense forests with streams or small rivers (Schiøtz 1967; Rödel 2003; Ernst and Rödel 2008). Unfortunately, some of the known Ivorian sites for *H. chlorosteus* no longer exist, such as Lakota (e.g., Schiøtz 1967), the Mount Péko National Park (Rödel and Ernst 2003), and the Cavally and Haute Dodo lowland forests in the western part of the country (Rödel and Branch 2002). In MNINR, the species was still found in abundance, but this study also registered the increasing and continuous degradation of its forest habitat.

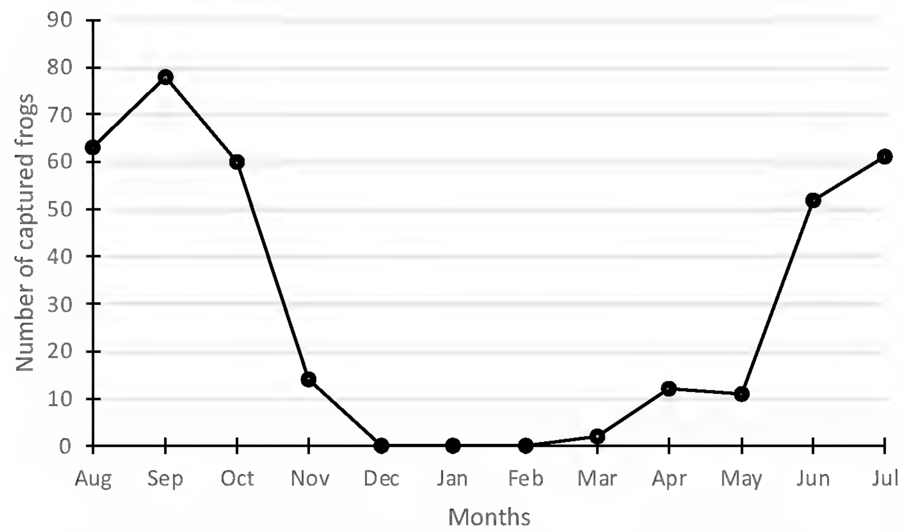

Fig. 8. Number of *Hyperolius chlorosteus* captured from 2 August 2019 to 8 July 2020 along lowland forest streams at Mount Nimba.

Conclusions and Threat Status

This study revealed the most viable and largest population of *H. nimbae* known thus far. However, it also revealed that formely known sites are most likely gone, and the one reported herein might be the last site where the species is thriving. Amphibians currently have no official protection status in Ivory Coast, and no dedicated conservation policies apply to them. The only existing conservation measures for their protection are the designations of protected areas (Rödel et al. 2021). Unfortunately, the small pocket of forest zone where *H. nimbae* was found falls entirely within a non-protected area, and consequently it is exposed to increasing and

Fig. 9. Variation of color pattern of *Hyperolius chlorosteus* from Mount Nimba Integrated Nature Reserve, western Ivory Coast.

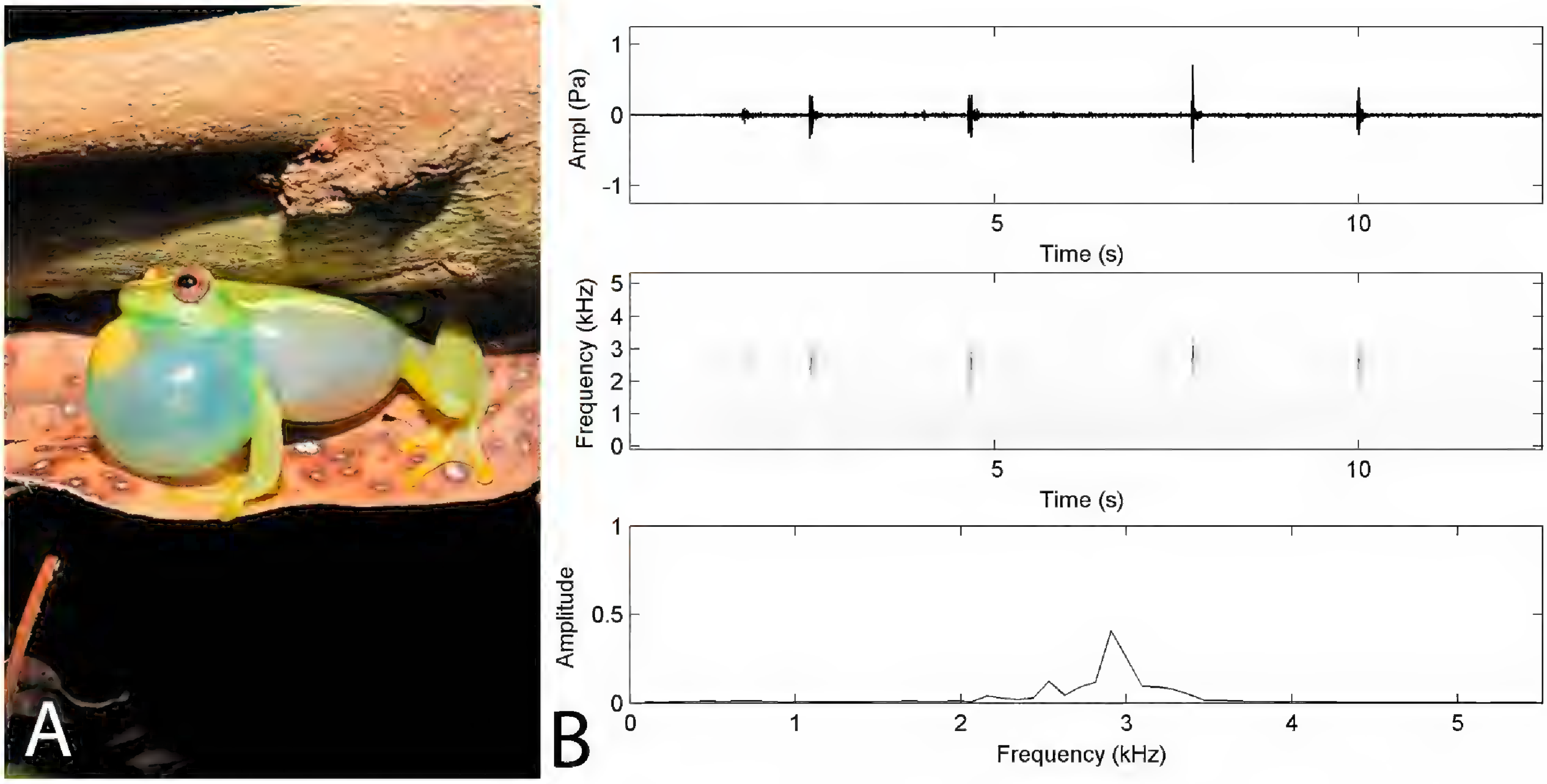

Fig. 10. Calling male of *Hyperolius chlorosteus* **(A)** with **(B)** waveform (above), spectogram (centre) and powerspectrogram (below), of the species' advertisement call, from Mount Nimba Integrated Nature Reserve. Note that the data for five calls are shown.

ongoing human influence. This species is thus facing an alarming risk of extinction, and the long-term persistence of its population in the forthcoming years is unlikely. The most important conservation action would be the immediate protection of its habitat at Yéalé, possibly accompanied by the establishment of a captive rescue population. Currently, *H. nimbae* is classified as Endangered (IUCN 2017). However, based on *IUCN Red List of Threatened Species* criteria A1(a) (population decline directly observed, only one known population remaining), B1 (extent of occurrence less than 100 km²), and B2 (area of occupancy less than 10 km², a: only one population known, b: population globally declining), we believe that the threat status of this species should be updated to Critically Endangered.

The second study species, *H. chlorosteus*, is similarly exposed to habitat loss due to intensive deforestation. The few remaining primary forests on which it depends do not enjoy sufficient protection or sustainable management (e.g., Chatelain et al. 1996; Wood 2003; Bakarr et al. 2004). The MNINR, Mount Sangbé, and the lowland rainforest of Taï National Park remain the three known Ivorian sites of *H. chlorosteus* at present (Rödel 2003; Ernst and Rödel 2008; Kanga et al. 2021). The recent *IUCN Red List* (2020) classifies *H. chlorosteus* as Least Concern. Given its large range, that category appears to be correct. However, based on the facts that in Ivory Coast the species only occurs in the westernmost parts of the country, several of the few national populations are gone, and the remaining forest habitats are declining, we think that *H. chlorosteus* should be regarded as Endangered nationally.

In summary, we urgently recommend the strict protection of the habitats of both species.

Acknowledgments.—We are greatly indebted to the Ministère de l'Environnement et du Développement Durable, and the Office Ivoirien des Parcs et Réserves, Direction de Zone Ouest, Côte d'Ivoire, for permitting the research. We would like to acknowledge the local populations of Danané villages for their hospitality, and are especially grateful for the support and collaboration from Paul Seu, elder of Kouan-Houlé. We thank Nicolas Granier, a conservationist of the Biotope Foundation France, for facilitating the relationships between the local people of Yéalé and our team. We are thankful to our local assistants and field guides Droh David Gueu and Zoda Alphonse Tokpa, for their invaluable help during the field expedition. Alan Channing and Lucinda Lawson improved our manuscript greatly with their constructive comments. We are grateful to Michael L. Grieneisen for his valuable comments.

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Kouassi Philippe Kanga is a recent graduate of the Université Jean Lorougnon Guédé (Daloa, Ivory Coast) with a Ph.D. in Herpetology. His work emaphsized amphibian diversity and its spatio-temporal dynamics in the Ivorian part of Mount Nimba. His research was under the direction of Dr. N'Goran Germain Kouamé, and aimed at linking amphibian assemblages with species function and assessing how species react in response to environmental changes in Mount Nimba.

Mark-Oliver Rödel works with his team at the Museum für Naturkunde, Berlin, Germany, where he is the Curator of Herpetology. He has studied the systematics, taxonomy, biogeography, and ecology of African amphibians for almost 30 years. With his group, comprising students from around the world, he currently runs projects in Germany, Ecuador, Guinea, Ivory Coast, Cameroon, and Mozambique. His special interest is on how species and ecological communities react to environmental changes. He has authored or co-authored about 400 scientific and popular publications, including several books.

Appendix 1. Counts of *Hyperolius nimbae* individuals captured in a heavily degraded site (07°31.928'N, 008°25.401'W; 425 m asl) at Yéalé from 2 August 2019 to 8 July 2020.

	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Night 1	11	7	10	4	2	1	1	2	2	4	5	7
Night 2	7	5	8	2	0	1	1	3	1	2	3	6
Night 3	9	9	5	1	0	1	2	2	3	4	5	3
Night 4	10	10	7	1	3	0	1	1	4	1	5	1
Night 5	11	11	5	1	2	0	0	1	3	2	6	7
Night 6	6	7	9	1	0	0	0	1	2	3	6	5
Night 7	7	6	6	1	2	0	0	1	2	1	1	6
Total	61	55	50	11	9	3	5	11	17	17	31	35

Appendix 2. Counts of *Hyperolius chlorosteus* individuals captured along forest streams at Mount Nimba Integrated Nature Reserve (MNINR: 07°34.652'N, 008°24.966'W; 716 m asl) and Yéalé (07°31.932'N, 008°25.508'W; 387 m asl) from 2 August 2019 to 8 July 2020.

		Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Night 1	MNINR	9	10	8	0	0	0	0	0	0	0	8	6
	Yéalé	1	0	1	0	0	0	0	0	0	0	0	0
Night 2	MNINR	7	9	7	1	0	0	0	0	1	0	9	7
	Yéalé	0	1	1	0	0	0	0	0	0	0	0	0
Night 3	MNINR	9	13	6	1	0	0	0	0	4	3	5	9
	Yéalé	0	0	0	0	0	0	0	0	0	0	0	0
Night 4	MNINR	7	12	10	1	0	0	0	0	2	3	12	9
	Yéalé	0	1	0	0	0	0	0	0	0	0	0	0
Night 5	MNINR	8	9	10	3	0	0	0	0	1	1	3	14
	Yéalé	2	0	0	0	0	0	0	0	0	0	0	0
Night 6	MNINR	7	9	8	5	0	0	0	1	0	1	8	9
	Yéalé	3	0	0	0	0	0	0	0	0	0	0	0
Night 7	MNINR	9	13	9	3	0	0	0	1	4	3	7	7
	Yéalé	2	0	0	0	0	0	0	0	0	0	0	0
Total		64	77	60	14	0	0	0	2	12	11	52	61

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Amphibian & Reptile Conservation
16(2) [General Section]: 104–119 (e319).

Goliath Frog (*Conraua goliath*) abundance in relation to frog age, habitat, and human activity

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***Abstract.*—Habitat change and overexploitation are major factors driving species population declines worldwide, and they often act in union. The Goliath Frog, *Conraua goliath,* is an iconic species that is known to be extensively exploited by humans. However, Goliath Frog populations have not yet been assessed quantitatively in relation to their proximity to human settlements, nor has the loss of terrestrial habitat adjacent to the frogs' riverine habitat been investigated. In this study, populations of the Goliath Frog were assessed across its range in Cameroon during nocturnal, time-constrained, visual encounter surveys. Goliath Frogs showed a patchy distribution along torrent rivers in three main habitat types: primary forest, secondary forest, and agroforestry plantations. There were no significant differences in the encounter rates among the three habitat types. However, we noted higher frog abundances, including larger sized adults, with increasing distance from human settlements, an observation confirmed by local frog hunters. Our observations revealed strong segregation in microhabitats with respect to age classes, as juvenile frogs were frequently found along river beds with rock pools/rock crevices, while sub-adults were mostly encountered around exposed rocks at river rapids, and adults were mostly recorded near cascades and waterfalls. The adults predominately perched on rocks around waterfalls and rapids, with distances of about 3–5 m between them, suggesting both territoriality and site fidelity. Adults were observed foraging at night, beyond 10 m from the river bank. During the day, adults were seen basking on rocks along the river bank. The lower abundance and size of Goliath Frogs near human settlements indicates the effects of hunting pressure, with terrestrial habitat showing less of an effect on this species. Monitoring of the remaining Goliath Frog populations, raising local awareness on the effects of hunting and habitat preservation, as well as law enforcement, are suggested as further efforts to conserve the world's largest frog species.**

Keywords. Amphibia, Anura, Cameroon, conservation, exploitation, habitat choice, monitoring, threatened species

Citation: Gonwouo NL, Schäfer M, Tsekané SJ, Hirschfeld M, Tchassem FAM, Rödel M-O. 2022. Goliath Frog (*Conraua goliath*) abundance in relation to frog age, habitat, and human activity. *Amphibian & Reptile Conservation* 16(2) [General Section]: 104–119 (e319).

Accepted: 29 August 2022; **Published:** 15 November 2022

Introduction

The world's biodiversity crisis is almost exclusively due to human activities, most notably the conversion and destruction of natural habitats. However, the overexploitation of many species, such as for food, is an increasingly serious threat as well. Frogs are no exception to this trend (Mohneke et al. 2010; Altherr et al. 2022), and both of these threats may also affect the world's largest frog, *Conraua goliath* (Boulenger 1906). This species is restricted to southwestern Cameroon and northern Equatorial Guinea, where it occurs in lowland to mid-altitude rainforests below 1,000 m asl (Lamotte and Perret 1968; Sabater-Pi 1985; Wild et al. 2004; Stuart et al. 2008; Channing and Rödel 2019). This frog is associated with fast flowing rivers and larger streams with rocky outcrops, rapids, and waterfalls (Perret 1957; Amiet 1975; Sabater-Pi 1985; Gewalt 1996; Herrmann et al. 2005). These natural habitats are becoming progressively altered through various human activities, such as conversion to farmland, construction of roads and hydroelectric dams, and exploitation for artisanal and commercial timber resources. The combination of logging and conversion of the remaining forests to agroforestry plantations has tremendous negative consequences on biodiversity, including amphibians. The

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progressive fragmentation of original forest landscapes leads to modified microclimates with obvious adverse effects on amphibian communities (e.g., Ernst et al. 2006; Stuart et al. 2004, 2008; Ernst and Rödel 2008; Hillers et al. 2008; Ofori-Boateng et al. 2013). Previous studies suggested that fragmentation and destruction of habitat has led to a reduction in Goliath Frog populations at various Cameroonian sites (Amiet 2004; Herrmann et al. 2005). If this is true, it is likely that these processes would cause general population decline over the entire range of the species. In addition, frog meat may be an important (or at least a much valued) protein source for many indigenous people throughout the Goliath Frogs' range (Gonwouo and Rödel 2008). Hence, the increasing human population, expansion of settlements and increased efficiency of hunting tools will intensify the pressure on this species. This is especially evident in the professionalized hunting methods (traps, hooks, spears, throwing nets, etc.) that have been developed specifically to collect Goliath Frogs (Amiet 2004; Gonwouo and Rödel 2008; Schäfer et al. 2019). The hunt for subsidiary consumption, as well as for local bush meat markets, might be one of the main factors driving the population decline of Goliath Frogs. The commercial harvesting of *Hoplobatrachus occipitalis* has contributed to the population decline of this species in northern Bénin (Mohneke et al. 2010). Based on its rarity and much larger size (assuming a longer time until frogs become mature), similar or even more severe consequences may be assumed for the Goliath Frog. As a result of these pressures, this species is currently listed as Endangered by the IUCN and Class A under Cameroonian law (IUCN Amphibian Specialist Group 2019a; NLG et al., unpub. data).

Previous studies on the Goliath Frog have focused mostly on its distribution (Perret 1957, 1960; Sabater-Pi 1962, 1967; Amiet and Perret 1969; Gewalt 1977), taxonomy, and phylogeny (Lamotte and Perret 1968; Nguiffo et al. 2019; Blackburn et al. 2020). Some investigations have also investigated various aspects of life-history, including larval development, parasites, and reproduction (Lamotte et al. 1959; Perret 1957, 1960; Sabater-Pi 1985; Nguiffo et al. 2015). Parental care has recently been documented in the species (Schäfer et al. 2019), and additional studies by the authors of this paper are in progress to further improve our knowledge of the life-history of this species. However, very little is known concerning the population trends and habitat preferences of this species, or the specific threats that this species is facing. In the absence of research on the habitat requirements and responses to the various threats facing the Goliath Frog, the development and implementation of appropriate conservation measures are difficult.

To remedy this general lack of knowledge, this study examines the impact of land use and proximity to human settlements on the relative abundance, demographics, and body size of Goliath Frogs. The data presented in this paper are based on six years of investigations on the Goliath Frogs in Cameroon, and allow us to examine the correlations between this species and human-caused forest alteration and to propose the directions and goals of future research and conservation strategies.

Material and Methods

Study Area

Fieldwork was carried out from November 2014 to December 2019 during both rainy and dry seasons (Table 1), although the dry seasons (November to February) were emphasized as the rivers were more accessible. Fieldwork focused on the areas around three main localities in south-western Cameroon: Moungo, Sanaga maritime, and Nkam division (Littoral region); Nyong-Ekele (Central region); and Bipindi in Ocean division (South region) (Fig. 1). In total, 13 rivers (Table 1) were surveyed, including the Nkam and Sanaga rivers.

Investigations were carried out from near sea level around Kribi (Ocean division), up to the foothills of Mount Manengouba near Nkongsamba (Moungo division). The latter locality hosts the northernmost population of the Goliath Frog and is characterized by several large rivers and streams. Overall, the landscapes of our sites constituted mostly low to medium elevation habitats, with the elevations of our frog observations ranging from 39 m asl along Lobe River (Bifa, Ocean division) to about 677 m asl along Nkam River (Nkoungsou, Moungo division). Other than the Moungo area, which is characterized by a heterogeneous, mountainous landscape (Mts. Kupe, Nlonako, Manengouba), the remaining sample localities have a low-rise or flat relief, only rarely interrupted by hills. The study areas comprised a mixture of several large forest patches of Guinea-Congolian lowland rainforest (both pristine and logged), agroforestry plantations, and small-scale subsidiary agricultural sites. Especially in the area around Yabassi (Nkam division), logging companies commercially exploit timber for exportation, despite the remoteness and difficulty in accessing the area. The entire study region has a tropical climate, with the wet season extending from March to October and the dry season from November to February. Rainfall peaks in August and September, and the driest period extends from late December to the end of February. The annual precipitation ranges from 2,000 to 3,000 mm (Amiet 1975).

Surveys and Data Acquisition

The visual encounter survey (VES) method (Heyer et al. 1994; Rödel and Ernst 2004) was used in suitable habitats to systematically survey for Goliath Frogs. The VES consisted of counting all Goliath Frogs encountered in every major habitat type, and provided an encounter rate per person-hour. Three major habitat types were

Table 1. River sites investigated for Goliath Frogs in three surveyed habitat types in western Cameroon. The information provided includes river name, total length of sampled trails, geographic position, and a short habitat description (including length of river investigated and the total sampling effort per site in person-hours).

Locality (river name, coordinates, elevation [m asl])	**Date**	**Habitat characteristics (including approximate length surveyed for each section and person-hours of effort for each site)**
Lobe 02°36'47.23"N, 10°01'05.51"E; 39 m asl	17 December 2014	Section one: Composed of logged secondary forest (SF) with open to semi-closed canopy forest which covered about 70% of the surveyed trail, ~250 m. Section two: Small-scale cocoa plantation with few native trees interspersed in the plantation and a relatively open canopy, ~150 m **(9.77 person-hours).**
Nkebe 4°45'25.05"N, 9°58'06.18"E; 231 m asl	14 February 2015	Section one: River bank bordered by primary forest with a closed canopy of native trees that were about 25–30 m high. Open understory including leaf litter on floor. Steep flanks at some sites that were difficult to access, with no signs of human activity, ~1,500 m. Section two: Selectively logged secondary forest along a path with constant human signs. Trees about 25 m high with relatively open to closed canopy. Secondary growth trees observed where logging had been carried out, ~400 m **(13.74 person-hours).**
Ekomtolo 4°47'32.57"N, 9°53'11.60"E; 332 m asl	12 February 2015	Section one: Composed of logged forest along steep portions of the river where farming activities are impossible. Many footpaths present and rampant wood extraction for local furniture and domestic fuel, ~300 m. Section two: Composed of large- to small-scale cocoa plantations with few native trees spaced all over the area and constantly managed by the community. Chemicals used to sustain the crops are processed in the nearby river with possible contamination, ~500 m (**4.25 person-hours**).
Dibombe 4°36'43.46"N, 9°46'42.26"E; 60 m asl	15 February 2015	Forest composed of a mosaic of primary forest, secondary forest, and agroforestry plantation interspersed all through the surveyed trail. Section one: Mainly closed canopy of native trees, about 25–30 m tall, along difficult-to-access terrain, no previous logging had occurred. Forest floor with about 70% leaf litter cover, ~900 m. Section two: Old selectively logged forest, easy access due to the many footpaths present, empty cartridges left behind by hunters, ~400 m. Section three: Small-scale plantation, mainly composed of cocoa and banana plants which covered the flat sections along the river on both flanks, ~300 m (**14.26 person-hours**).
Sanaga Ngo Mpem 4°04'15.42"N, 10°40'14.16"E; 241 m asl	7–12 July 2016	Section one: Primary forest on slopes along the river where movement and tree exploitation is difficult, ~1,000 m. Section two: Included portions where access was easier with several human foot paths present, signs of forest exploitation, ~650 m (**10.55 person-hours**).
Sanaga (Tributary River) 4°03'23.19"N, 10°37'12.88"E; 297 m asl	13–15 July 2016	Section one: Composed of small patches of native large trees around difficult-to-access points of the river, bordered by very large rocks, ~700 m. Section two: Composed of recently logged forest patches, with several hunting paths. Frequent use of the forest to collect non-timber forest products, ~600 m (**14.55 person-hours**).
Keinke 2°52'36.73"N, 10°04'56.75"E; 48 m asl	2–3 March 2017	Section one: Consisted of closed canopy trees of about 25 m in height on both sides of the river. Footpaths present within the forest seem to be regularly used by fishermen and Goliath Frog hunters, ~900 m. Section two: Recently logged forest with open canopy and bushy understory. Regular use of this forest section evident, with many footpaths present, ~200 m (**11.72 person-hours**).

Table 1 (continued). River sites investigated for Goliath Frogs in three surveyed habitat types in western Cameroon. The information provided includes river name, total length of sampled trails, geographic position, and a short habitat description (including length of river investigated and the total sampling effort per site in person-hours).

Locality (river name, coordinates, elevation [m asl])	Date	Habitat characteristics (including approximate length surveyed for each section and person-hours of effort for each site)
Magamba 4°45′19.03″N, 9°52′16.68″E; 308 m asl	6 April 2016	Trail bordered by agroforestry plantations as well as subsistence plantations on both banks. Fallow land present along river bordered by degraded forest with very dense vegetation, edges with shrubs and only a few trees present, ~600 m **(6 person-hours)**.
Nkam 5°08′17.43″N, 9°59′43.17″E; 677 m asl	29 October –2 November 2018	Section one: Consisted of agroforestry plantations, mainly cash crops including coffee, cocoa, and palm oil trees growing on the river bank, ~800 m. Section two: Mainly composed of small relic forest patches on steep valleys along the river, access was difficult. No possibility of farming at this site, but forest patches appeared to have been logged with several foot paths found, ~350 m **(4.96 person-hours)**.
Mbo 4°49’39.16”N, 9°47’18.58”E; 465 m asl	6 April 2016	Section one: Vegetation composed of a mosaic of secondary forest and agroforestry plantations on both river banks. Secondary forest composed of fallow land, more than 10 years old, and several cocoa plants and large palm trees could still be found. Section two: Permanently cultivated plantation with young cocoa and palm trees, intensively managed with signs of constant human presence, ~250 m **(14.97 person-hours)**.
Mpoula 4°38′15″N, 9°43′07″E; 200 m asl	27 February – 5 May 2018	Surveyed trail composed of a mosaic of secondary forest (~200 m) and agroforestry plantation (~300 m) on both sides of the river, constant human activities noted along the trail **(10.8 person-hours)**.
Njuma 4°20’53.1”N, 10°13’56.3”E; 304 m asl	27 August –17 September 2019	River bordered by primary forest (~1,200 m) on both sides with little or no signs of human activity, though foot paths where present and have been used by poachers and seasonally by Goliath Frog hunters **(5.31 person-hours)**.
Bisoue 4°21’38.3”N, 10°12’30.4”E; 152 m asl	27 August –17 September 2019	River bordered by primary forest (~ 400 m) on both sides with little or no human impact. Access was difficult at some points due to the dense undergrowth along old footpaths **(15 person-hours)**.

identified along the 13 rivers: primary or pristine forest (PF; Fig. 2A), selectively logged or secondary forest (SF; Fig. 2B), and agroforestry plantations (AP; Fig. 2C, also see Table 1 and below for detailed descriptions of the habitat types).

Transects along the rivers could comprise either a single vegetation type, or a mosaic of different vegetation types or segments (e.g., PF, SF, and AP) that could vary considerably in short succession. This was especially true when human settlements were nearby. To measure the portion of a certain vegetation type in a single transect, we passed the respective segment and measured the covered distance with a GPS unit. The vegetation type was identified on both sides of the river by assessing the canopy cover (visual estimation to 25% accuracy), estimated height (± 5 m), and measured diameter at breast height (DBH) (± 0.5 cm) of the trees, as well as any obvious human impacts, such as selective logging, hunting, or extraction of non-timber forest products (e.g., leaves, tree bark, fruits, resins, or roots).

Primary Forest (PF) consisted of closed canopy forest with 75–100% canopy cover. This forest type was dominated by large, native trees of about 25–30 m in height, although the largest exceeded 50 cm in DBH. No evidence of recent logging was present in PF. Although hunting or fishing paths were regularly found along the rivers (especially close to human settlements), revealing some degree of natural resource exploitation, this forest type was still considered mature and relatively undisturbed. Primary Forest comprised seven segment portions of the 13 rivers surveyed, and their lengths and brief descriptions are provided in Table 1.

Selectively logged Secondary Forest (SF) included all vegetation formations with a relatively closed canopy (50–75% canopy cover) and medium to large trees (10–25 m in height). Here, the tree composition included both native and non-native tree species with DBH usually exceeding 40 cm, including many secondary growth trees. These forests had been previously logged for commercial timber exportation, and/or by the local

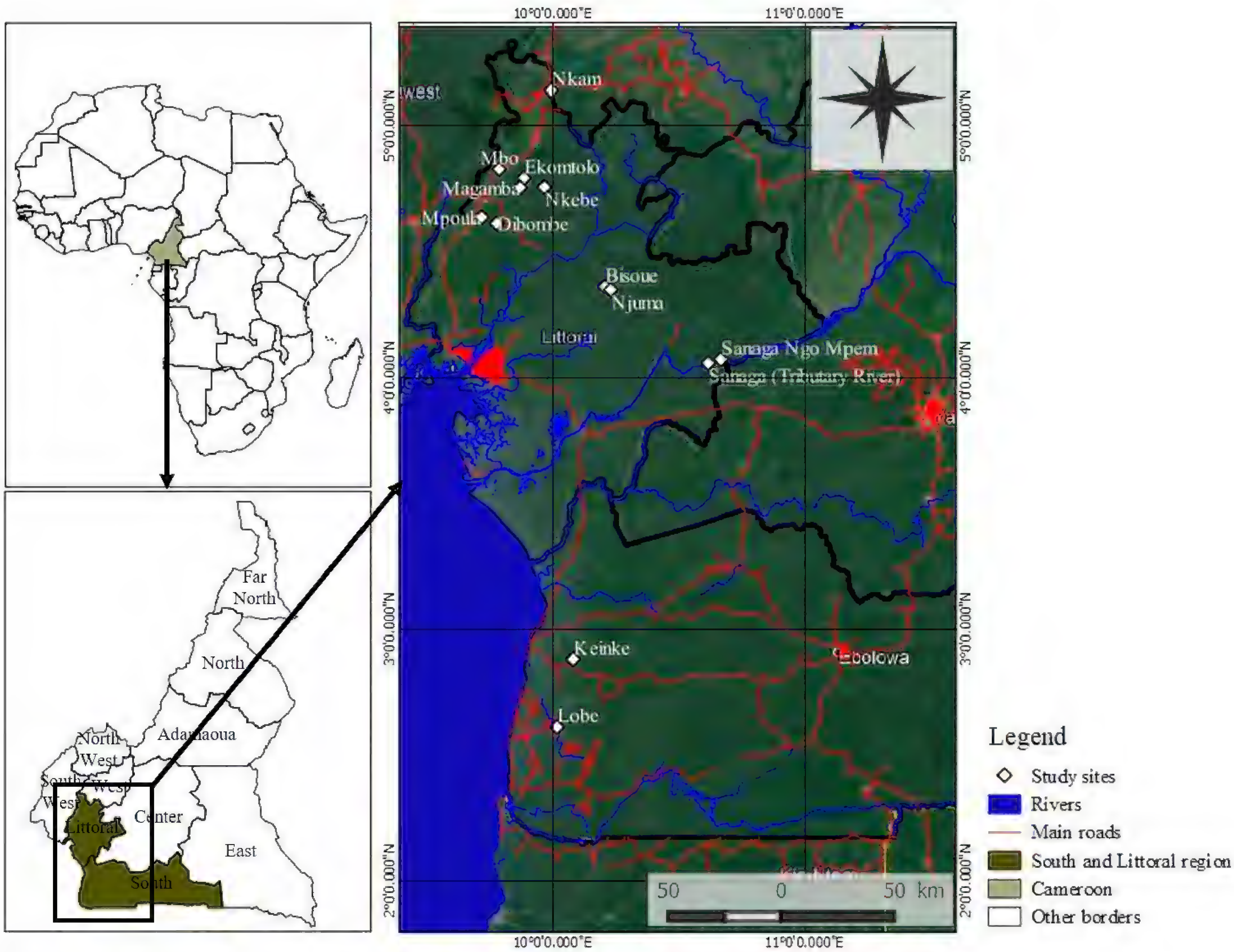

Fig. 1. Map of Cameroon indicating the locations of the study sites.

population for house construction or for local trade. Many footpaths, as well as the remains of abandoned logs, snare traps, and rifle cartridges, were found within these forests, indicating ongoing and constant use for hunting and timber exploitation. Secondary Forest comprised ten segment portions of the 13 rivers surveyed.

Agroforestry Plantations (AP) included all plantations, ranging from small-scale subsidiary crops and/or cash crops cultivated by the local people to intensively farmed, large-scale monocultures created by international commercial agro-companies. This habitat type, especially when cultivated by local farmers, could include native trees with more or less open canopies (≤ 50%), the largest stem diameters exceeded 40 cm, and they were spaced all throughout the cropped species. Most of the cultivated plants were introduced species, including manioc (*Manihot esculenta*), papaya (*Carica papaya*), pineapple (*Ananas comosus*), mango (*Mangifera indica*), cocoa (*Theobroma cacao*), palm oil (*Elaeis guineensis*), avocado (*Persea americana*), and bananas (*Eumusa* spp.). Native large trees were found mostly in cocoa plantations as shade-trees, whereas banana tended to be cultivated in large monocultures. The latter is cultivated at a commercial scale in the Njombe-Penja area for exportation. Agroforestry Plantations comprised seven segment portions of the 13 rivers surveyed. To enhance crop production, herbicide and pesticide mixtures are prepared in nearby rivers and streams with likely runoff, polluting the rivers.

Sampling took place between 0700 and 1200 h, and included various microhabitats, such as waterfalls, rocky rapids, rock pools, and riverbanks, as well as forest strips up to 20 m from the rivers. Gaining access to the rivers and their banks demanded careful clearance of trails, e.g., removing of some lianas or dead wood along a narrow trail. Trails were set-up at least 24 h before surveying the respective area. To maximize the probability of documenting all individual frogs, teams of two or three researchers walked along the rivers at a slow, steady rate of 0.2 m per second, avoiding any jerky movements that could disturb the frogs. Headlamps and handheld flashlights were used to detect the frogs, particularly by picking up eye-shine. All spatial data were recorded with a Garmin GPS (60 cx; accuracy of 5–10 m). For every frog, the perch site, date, time, posture, size, and distance from the riverbed were recorded. Size categories were classified as follows: adults (≥ 19 cm snout-vent length) (Fig. 3A); subadults (approx. 10–18 cm) (Fig. 3B); and juveniles (≤ 9 cm) (Fig. 3C).

Daytime habitat assessments preceded the nighttime

Fig. 2. Examples of the three different forest types investigated in this study: **(A)** primary forest (River Dibombe), **(B)** secondary forest (River Nkam), and **(C)** agroforestry plantations (River Mpoula).

surveys, with notes taken on habitat features, such as dominant vegetation, as well as notable, anthropogenic influences on the sites. Notes on the microhabitats of sun-basking frogs were made accordingly. Data for the daytime searches are not generally comparable to the nighttime searches, given that the frogs are mostly active during the night. However, the locations of daytime frog encounters regularly coincided with the presence of similarly-sized individuals during the night.

Local Ecological Knowledge (LEK) was obtained from local frog hunters around the surveyed areas who could reliably identify Goliath Frogs and regularly hunt them. This information was collected through informal interviews and discussions, and it greatly contributed to our assessments. To prevent any biasing toward certain answers, we asked all of the respondents the following six questions: Which are the rivers where Goliath Frogs are present? How far are they from the village? What was your biggest catch ever, and when was that? What was your biggest catch in 2019? How often do you hunt for the frogs? What is your perception about the Goliath Frog population around the village?

Data Analysis

The sampling effort was recorded only for the nocturnal surveys. Daytime searches were not time constrained as they were mostly meant to identify nocturnal survey sites. Sampling effort is given in person-hours, i.e., the number of hours spent surveying multiplied by the number of observers for any given river and habitat type (Table 2). The relative abundance of frogs was calculated as the number of individuals observed per time unit, divided by the number of sightings through the total sampling effort for each river or habitat type, and given as frogs per person-hour. As the relative abundances of Goliath Frogs were not normally distributed, Pearson's Correlation Coefficient was applied to compare the abundance of frogs and age groups per habitat type.

In order to examine frog abundance in relation to human presence, the GPS coordinates of the study sites were used and a 10 km buffer around each point was drawn in a geo-information system (QGIS Development Team 2021). All streets and settlements within the buffer zone were extracted from the Open Street Map database (https://planet.openstreetmap.org), and the total length of all roads (motorways, interregional and regional highways, urban as well as agricultural roads) was determined, as well as the number and type of settlements. No recent, fine-scale census data are available for the study area, thus the human population within each buffer zone was estimated by assigning fixed values to each of the different settlement types. Hamlets, the smallest type of settlement, accounted for 200 people, villages for 1,500, towns for 25,000, and cities for 100,000 inhabitants. Note that these values were

Fig. 3. The three different age sizes of Goliath Frogs considered in this study: **(A)** adult (≥ 19 cm), **(B)** subadult (10–18 cm), and **(C)** juvenile (≤ 9 cm).

based on the open street maps criteria. Human population density was calculated by dividing total population by the area within the 10 km radius buffer zone (314 km²). The distance of each sampling site to the nearest road and settlement boundary were determined. Subsequently, the data were screened for any linear dependencies of the GIS extracted values and the number of observed frogs (*iph*) in a regression analysis. Distance measures were log-transformed before the analysis.

To analyze the LEK data, a Welch-test comparing the hunter's perceived frog weights in different years was performed. A linear regression model was used to determine if there was a correlation between frog weight measured by local hunters and distance to the nearest settlement. All analyses were conducted using R v.4.0.0 (R Development Core Team 2014).

Results

Encounter Rates and Distances to Settlements and Roads

A total of a 100 person-hours were spent surveying for Goliath Frogs at 13 rivers across the entire range of the species in southwestern Cameroon. During the study, 490 frogs were observed along 26.7 km of riverine habitats, including 13.1 km in PF, 7.0 km in SF, and 6.6 km in AP. The number of person-hours spent on each habitat type varied, given the differences in river size and habitat accessibility. The encounter rates of frogs varied with respect to habitat types, rivers, and with grade of anthropogenic influence. For the entire study period, the average encounter rate was five frogs per person-hour (5 *iph*). Within the three habitat types, the highest mean *iph* was 8.2 recorded in SF, followed by 7.1 in PF, and 4.6 in AP. However, these values were not statistically different (Fig. 4). The two individual study sites with the highest encounter rates (17.0 *iph*) were both in SF, along the Sanaga and Keinke rivers. At these sites, the forest had been legally and commercially logged. These localities are far from human settlements and the frogs seemed to show lower flight-distances when approached compared to the frogs at other sites (however, we did not collected data to support this general impression). The lowest encounter rates were along the Ekomtolo and Mpoula Rivers (1.0 *iph*), and both localities are close to human settlements. Although disturbed, the surveyed portion of Mbo River, which is bordered by about 50% AP, revealed very high encounter rates (8.4 *iph*).

Human densities and the levels of anthropogenic disturbance varied considerably around the study sites. Total road length within a 10 km radius buffer around the sites ranged between 9 km and 168 km, with a mean of 84.5 km. The number of settlements ranged from 1 to 20 within the buffers, with a mean value of 10.1. The estimated human population densities ranged from

Table 2. Encounter rates of Goliath Frogs (in person-hours of searching effort) during time-constrained visual encounter surveys in the three different habitat types: PF, primary forest; SF, secondary forest; and AP, agroforestry plantation. Data are given for each of three different age sizes: a, adult; s, subadult; and j, juvenile.

Habitat type	**PF**				**SF**				**AP**			
Age size	**a**	**s**	**j**	**Σ**	**a**	**s**	**j**	**Σ**	**a**	**s**	**j**	**Σ**
Lobe					7.20	2.40	0.00	**9.60**	4.00	6.00	0.00	**10.00**
Nkebe	2.07	1.33	0.93	**4.33**	2.75	2.25	0.50	**5.50**				
Ekomtolo					1.00	0.00	0.00	**1.00**	1.80	0.80	0.20	**2.80**
Dibombe	3.50	2.33	1.33	**7.17**	3.00	1.88	4.13	**9.00**	2.00	2.50	0.00	**4.50**
Sanaga Ngo Mpem	2.40	1.05	1.05	**4.50**	2.77	2.08	1.62	**6.46**				
Sanaga (Tributary River)	6.43	4.29	1.71	**12.43**	9.00	6.50	1.50	**17.00**				
Keinke	3.67	5.67	1.33	**10.67**	9.00	7.50	0.00	**16.50**				
Magamba									0.89	0.78	0.33	**2.00**
Nkam					4.29	2.57	0.00	**6.86**	2.63	1.50	0.00	**4.13**
Mbo					4.20	1.20	1.20	**6.60**	2.40	4.20	1.80	**8.40**
Mpoula					2.17	0.33	1.00	**3.50**	0.44	0.00	0.22	**0.67**
Njuma	1.63	1.25	0.00	**2.88**								
Bisoue	3.38	4.50	0.00	**7.88**								
Mean	**3.29**	**2.92**	**0.91**	**7.12**	**4.54**	**2.67**	**0.99**	**8.20**	**2.02**	**2.25**	**0.37**	**4.64**

1,000 to 99,200 inhabitants in the 314 km² of the buffer zones (12.7–1,263.7 persons per km²), with a mean value of 32,592.3 (415.2 persons per km²). Road length and population density were negatively, but not significantly, associated with higher frog numbers (Table 3). The distances between study sites and the nearest settlement ranged from 89 to 9,114 m (median = 2,741 m), and the distances between study sites and the nearest road ranged from 176 to 8,653 m (median = 701 m). While both measures (after logarithmic transformation) indicated a positive association between distance and frog numbers, only the nearest settlement showed a robust and significant linear dependency (Table 3, Fig. 5). In other words, more frogs were found when the nearest settlement was farther away. Only the Njuma River violated this rule, as it was the most remote site but only provided a small number of frogs (Table 3).

Age Categories and Microhabitats

Of the 490 Goliath Frog observations, 243 (49%) were adults, 170 (35%) were subadults, and 77 (16%) were juveniles. Of all the adults, 48% where from PF, 36% from SF, and 16% from AP. The encounter rates of the three age sizes varied among the rivers, as well as both between and within the different habitat types. A Chi-square test of the three age groups showed that there was no difference in the population structures between the three different habitat types ($\chi^2 = 3.48$, $df = 2$, $p = 0.48$). The highest encounter rates among the three age sizes were for adults (9.0 *iph*) recorded in SF; while the lowest was in juveniles (1.0 *iph*) recorded in all three habitats (PF, SF, and AP). The recorded encounter rates of the frogs, sorted by age sizes within the three surveyed habitat types, are summarized in Table 4.

Goliath Frogs showed a patchy distribution across the study sites and were mostly restricted to particular microhabitats, which included moderate to fast flowing rivers with cascading, turbulent rocky sections (Fig. 6), or waterfalls with mostly sandy soils. The species was recorded from Bifa, Babong, Ekomtolo, Magamba, Manengotang, Nko-Olong, Ngo-Mpen, Nkongsou, and Sole. The altitudinal range of the inhabited sites spanned from 39 m asl at Lobe River around Bifa and near the coast, to about 677 m asl at Nkam River. Goliath Frogs were recorded in 75% of the surveyed rivers, but only when these included suitable microhabitats. The inhabited river sections surveyed varied from 50 m to more than 300 m. The torrent, rocky sections were inhabited while the in-between sections, slow moving, meandering river parts with no rocks, revealed no frogs. Goliath Frogs were completely absent from rivers lacking fast flowing sections and rocks. For example, the five rivers south of the newly constructed deep-sea port at Kribi that were investigated all lacked the above-mentioned microhabitats, and yielded no Goliath Frogs despite being within the range of the species. Discussions with local ethnic groups, including the Bagyli/Bakola people who have lived in this forest for many generations, confirmed that Goliath Frogs never occurred in this area.

Age dependent differences were noted in microhabitat use. When Goliath Frogs came out at night to perch on rocks, the adults used the areas around large cascading waterfalls, while sub-adults were more often present on rocks in the rapids, and juveniles inhabited rock pools and crevices. Adult frogs were abundant around waterfalls

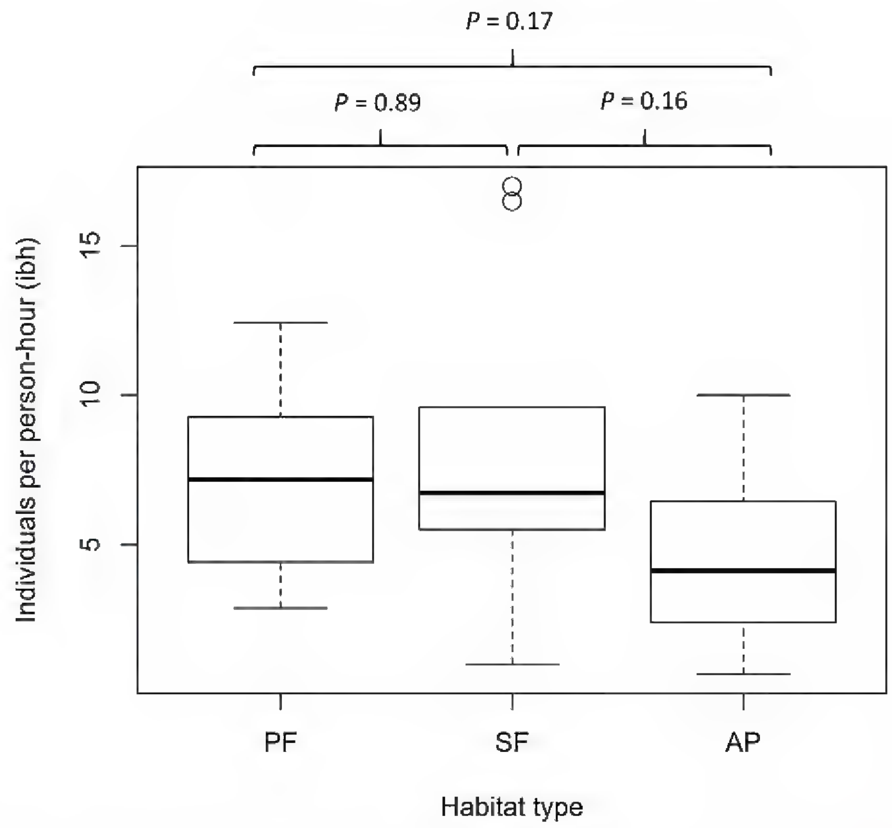

Fig. 4. Number of individual Goliath Frogs recorded per person-hour in each of the three surveyed habitat types: PF = primary forest; SF = secondary forest; AP = agroforestry plantation. Note that the encounter rates of frogs were not statistically different between any of the three habitat types.

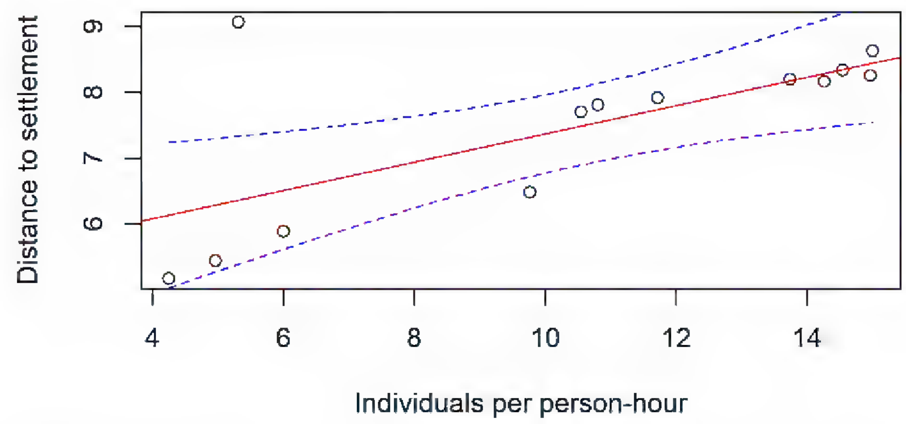

Fig. 5. Scatterplot of Goliath frog abundance (as individuals per person-hour) and log transformed distance to the nearest settlement. The red line is the trendline of the fitted linear model and the blue dotted lines demarcate the 95% confidence interval. Note that the top outlier point refers to Njuma River, which was the most remote site sampled, however, it also accounted for one of the lowest numbers of individuals.

Fig. 6. Typical forested and rocky-sandy riverbed characteristics for Goliath Frog habitat (Dibombe River).

but maintained some distance from one another. The closest distance between two adult frogs was 3 m, observed at Dibombe River. A maximum of seven adult individuals were observed at a single waterfall along Nkebe River. On Mpoula River, adult frogs were seen sitting on large branches within jumping distance of the stream (~5 m in adult frogs), at more than 2 m above the ground. At night, adult frogs that had fled from the surveyors by diving into the stream returned to the same perching rocks shortly (10 to 15 min) after disturbance, indicating fidelity to particular perching sites. Adults and subadults ($n = 24$) were frequently observed at night on low bushes and trees more than 10 m away from the riverbed. During the daytime, our observations revealed extensive sun-basking behavior, i.e., more than 20 adults were seen sun-basking throughout the study period. Adults often leaped and dove into the rivers upon our approach (flight distance 4 to 10 m). One individual was observed basking on the same rock on three consecutive days, along a relatively calm portion of Ekomtolo River. When disturbed, this frog jumped into the river and returned to its perch site after about 30 to 45 min.

Presence at Sites Impacted by Pollution and Agricultural Activities

The data revealed that Goliath Frogs persist in forest fragments, plantations, and rivers, even when surrounded by human settlements. Observations from the localities of Magamba and Manengotang indicate that small populations can be present at about 200 m from human settlements. Here, the habitat was patchy and comprised a mosaic of small forest remnants and small subsidiary plantations. The Goliath Frog occurrence at these places was also confirmed by Goliath Frog hunters, and frog hunting at these sites was perpetual. We commonly observed habitat pollution by the dumping of household waste into the rivers and adjacent forests. Unfortunately, there is no quantitative data regarding how long the habitats had been impacted (by logging and/or pollution); for how long and with what intensity the frogs had been/are being hunted; or how large the populations had been previously and how they had developed. Thus, there is no way to estimate how long these populations may prevail despite the small numbers of individuals and altered habitats.

The vast majority of the local people (~70%) around the study sites live on subsidiary and cash crop agriculture. In the study area, many forests along large rivers and streams have been transformed into cocoa and palm oil plantations, with larger portions converted where populations are high. To maintain these plantations and to improve production, fertilizers, herbicides, fungicides, and insecticides are used extensively. The preparation of those chemicals generally happens along the nearby rivers and streams, inevitably contaminating the water (NLG, pers. obs.). The scale of these potential threats

Table 3. Sample sites, numbers of frogs, and extracted values for number of roads, total length of roads, number of settlements, derived population estimate within the 10-km buffer zone, as well as measured distances to nearest settlement and road. Correlation coefficient and *P*-values from correlation analysis are given below each of the respective measures.

River	IPH	Total length of roads	Distance to nearest road	Distance to nearest settlement	Number of settlements	Population estimate
Lobe	9.77	167.9	650.9	701.26	5	1,000
Keinke	11.72	86.6	2,741.1	2,941.09	6	9,000
Dibombe	14.26	78.2	3,508.5	525.02	6	9,000
Bisoue	15.00	23.8	5,624.6	6,126.63	1	1,500
Mpoula	10.80	131.7	2,464.6	505.07	10	85,500
Nkebe	13.74	31.8	3,634.7	2,372.22	7	10,500
Sanaga (N)	10.55	69.4	2,199.6	2,236.13	5	31,000
Sanaga (T)	14.55	82.5	4,175.9	5,603.30	19	28,500
Njuma	5.31	8.9	8,653.5	9,113.55	1	1,500
Magamba	6.00	80.5	358.8	149.07	17	25,500
Ekomtolo	4.25	94.6	175.8	89.25	19	75,500
Mbo	14.97	82.2	3,843.3	541.14	15	46,000
Nkam	4.96	160.1	229.9	477.44	20	99,200
R^2		-0.257	0.688	0.431	-0.304	-0.415
P		0.3972	**0.0093**	0.1410	0.3130	0.1590

to the frogs varied through the study sites and time. Along the river at Magamba for instance, large quantities (estimated at around 70%) of the original forest were transformed into plantations within our six-year survey period. Nevertheless, the Goliath Frog populations persisted at these sites.

Frog Size and Distance to Settlements

Frog size, estimated by the authors and the surveyed hunters, was positively correlated with distance to settlements, with smaller frogs living closer to the settlements (Fig. 7). Discussions with 11 frog hunters revealed that they have to move increasing distances of 300 to 4,000 m from the settlement in order to find large frogs, and that the adult and subadult/juvenile Goliath Frogs, which were once common around waterfalls and rock pools, are now less abundant. Based on weight estimates from the hunters, they agreed that the largest Goliath Frog they ever encountered, estimated to weigh about 5 kg, was caught before the year 2010. There was a significant (Welch-test: $t = 6.14$, $df = 15.87$, $p < 0.0001$) drop in the perceived frog weight when compared to the largest frog caught in 2019 (Fig. 8).

Discussion

This study assessed Goliath Frog habitats and relative abundance over large parts of the known range of this species in Cameroon, in order to understand the influences of land use and vicinity to human settlements. Goliath Frogs were found to occur within all of the three main habitat types surveyed, i.e., primary forest, secondary forest, and agroforestry plantations. The frogs utilize a combination of particular microhabitats that are stratified by different age sizes. Torrent water and rocks seem to be requirements for the presence of all ages. Based on our data, Goliath Frogs seem to be able to deal with some degree of habitat alteration, and the population decline is mostly due to hunting.

Impacts of Anthropogenic Factors

Due to the lack of previous (quantitative) data, it is difficult to reliably assess whether and to what extent the Goliath Frog populations have changed. Therefore, we had to base our assessment on indirect evidence, e.g., the comparisons of frog occurrences in pristine versus altered habitats, the severity of different threats, and interviews with local frog hunters. One exception is the previously published data on the abundance of Goliath Frogs along the Sanaga River, described by Perret (1957, 1960) and Amiet and Perret (1969). These populations still persist today, despite the high degree of selective logging in the area. However, this positive finding does not preclude the fact that the species seems to be threatened by human activities in general, and the situation for many local populations is not very promising. We base this conclusion on our observation that especially large adult frogs are rare around human settlements and increase progressively farther away, a basic finding confirmed by the surveyed frog hunters. Two indirect measures of anthropogenic impact, roads and population densities, indicated a trend of increasing frog numbers with the remoteness of habitats, although only frog abundance and distance to settlement was robustly, positively correlated.

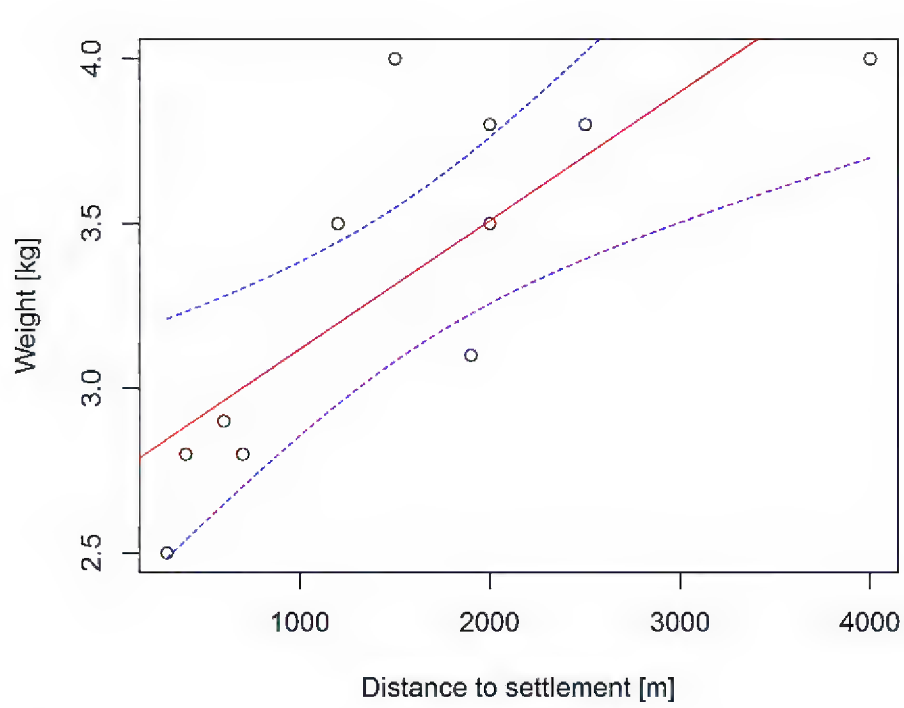

Fig. 7. Scatterplot of frog weight and distance to the nearest settlement. Note that the weight of the Goliath Frogs was increasing with distance from human settlements.

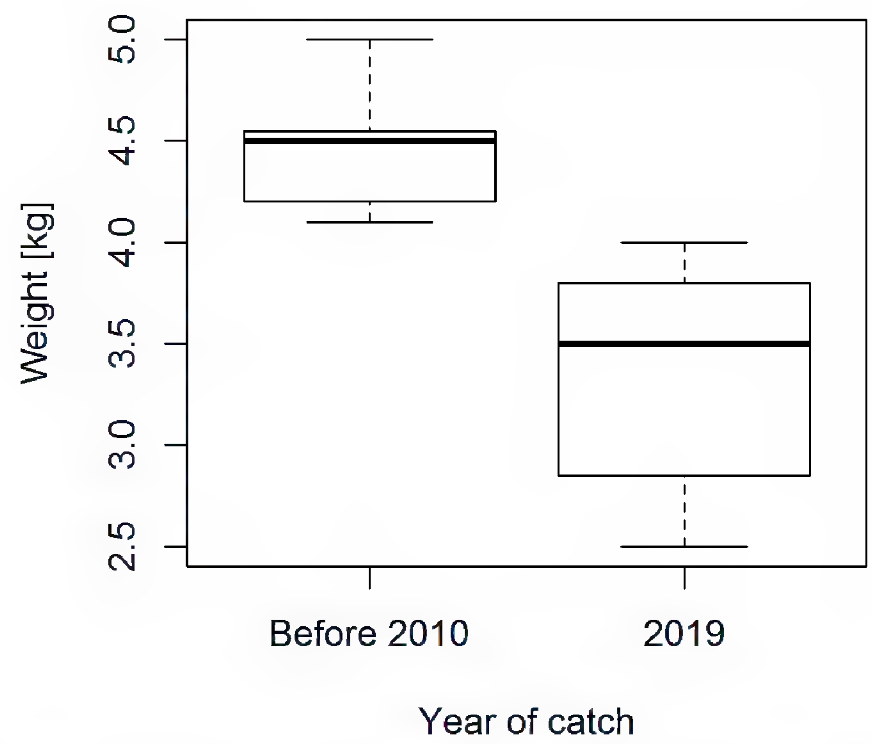

Fig. 8. Changes in weight of Goliath Frogs from around 1990 to 2019, as estimated by the surveyed frog hunters.

This analysis has some limitations. First, there are limitations in the dataset itself. For instance, we are certain that not all small settlements and roads were consistently recorded, and thus the human impact may be generally larger. Our population estimates include some errors and inaccuracies as well, e.g., the population for the category ‘village’ in OpenStreetMap ranges from 500–5,000. Clearly not every village will have a population of about 1,500 inhabitants. Nonetheless, our data generally indicated coherent patterns. The Goliath Frog population of Lobe, for instance, is situated right next to a vast banana plantation and gave the lowest frog population estimate. On the other hand, several Goliath Frog populations were quite large despite being in close proximity to major roads. Generally, the distance to the nearest settlement was a better predictor for frog abundance.

The impact of distance to the nearest settlement was especially notable for populations that are exploited for food and trade, and also comprise anthropogenic impacted habitats. For instance, the Nkongsamba area has undergone a drastic change in vegetation structure over the past decades, as large-scale agro-industrial plantations and an increasing number of subsistence plantations have

Table 4. Counts of the Goliath Frogs observed in the 13 rivers for the three habitat types (PF, primary forest; SF, secondary forest; AP, agroforestry plantation) across its range in Cameroon. Count data are provided with respect to the three different age sizes: a, adult; s, subadult; and j, juvenile.

River	Count data (numbers of observed individuals)												
	PF				SF				AP				Total
	a	s	j	Σ	a	s	j	Σ	a	s	j	Σ	
Lobe					6	2		**8**	2	3		**5**	13
Nkebe	31	20	14	**65**	11	9	2	**22**					87
Ekomtolo					3			**3**	9	4	1	**14**	17
Dibombe	21	14	8	**43**	8	5	11	**24**	4	5		**9**	76
Sanaga Ngo Mpem	16	7	7	**30**	12	9	7	**28**					58
Sanaga (Tributary River)	15	10	4	**29**	18	13	3	**34**					63
Keinke	11	17	4	**32**	6	5		**11**					43
Magamba									8	7	3	**18**	18
Nkam					5	3		**8**	7	4		**11**	19
Mbo					7	2	2	**11**	4	7	3	**14**	25
Mpoula					13	2	6	**21**	4		2	**6**	27
Njuma	13	10		**23**									23
Bisoue	9	12		**21**									21
Total	**116**	**90**	**37**	**243**	**89**	**50**	**31**	**170**	**38**	**30**	**9**	**77**	**490**

been established (NLG, pers. obs.). In this area, Goliath Frogs are also intensively hunted for the food market. This is the area where we recorded the lowest encounter rates throughout the entire study period. Habitat conversion and degradation usually went hand in hand with hunting pressure, with both being more pronounced close to settlements. Around the localities of the Ebo forest, anthropogenic pressure was almost absent, and here we encountered the highest numbers of frogs per survey effort.

Importance of Forest Habitats

In contrast to the human impact, vegetation type was not a useful predictor, as Goliath Frogs were present in all forest types from semi-open to close-canopy forests (as long as cascading rocky river sections were present). Goliath Frogs apparently need some forest, but not necessarily pristine forest. They live in cold water and regularly sun-bask, presumably to regulate body temperature. Thus, the opening of forest habitats and resulting raising of temperatures may not negatively impact them, as long as the water temperature remains "low enough" (although, unfortunately, the temperature preferences of the species are unknown) and the habitat surrounding the rivers can still provide enough food and shelter. Other African frog species with similar life-histories and inhabiting forested, torrent rivers, e.g., *Conraua alleni* and *Odontobatrachus* spp., also usually occur in cooler streams in forest, but may persist in areas with little riverine forest surrounded by savanna (Rödel 2003; Rödel and Bangoura 2004).

In this survey, when cascading, turbulent water with rocks and some forest patches was present, Goliath Frogs were reliably recorded. Thus, Goliath Frogs may be able to tolerate forest degradation to a surprising extent. This is in line with predictions by Hirschfeld and Rödel (2017) that large frogs in particular, with large clutch sizes and aquatic larvae, may be more resilient to forest degradation than species with other trait combinations. We would like to stress, however, that our observations should not be interpreted as indicating that riverine vegetation is not important for maintaining Goliath Frog populations.

Riverine forest may be important for Goliath Frogs during their nocturnal foraging activity. It is likely that all individuals observed along the river banks were adopting a 'sit and wait' foraging strategy. A study on stomach and intestinal contents revealed that the diet of *C. goliath* consists of approximately 60% arthropods, 20% crustaceans, 10% amphibians, and 10% indeterminate food items, the latter comprising ingested stones as well as pieces of wood and leaves (Sabater-Pi 1985). The majority of the arthropods were terrestrial taxa. The presence of leaves, wood, and stones also suggests a mainly terrestrial foraging mode. If the quality of the riparian forests impacts prey quality and quantity, this would likely impact the Goliath Frog populations as well.

Our observations on one particular frog highlight the Goliath Frog's use of riverine forest habitats. In primary forest along Nkebe River, a large adult was found in the forest leaf litter at about 14 m from the river. When disturbed, the frog covered this distance with three long jumps back to the river (also see Herrmann and Edwards 2006). In about 1 m water depth, the frog could then be spotted in the slow flowing, clear water. Further disturbance (with the torch beam) triggered the frog to bury itself deep in the sandy and leaf-littered river bottom until it could not be seen anymore, a behavior also known from its smaller congener, *C. crassipes* (Knoepffler 1985). Goliath Frogs are less active during the day, and when encountered, they were usually found sun-basking. When disturbed, the behavior was the same as during the night, with the frog seeking shelter in the water or beneath the rocks it was sitting on.

Use of Microhabitats by the Different Age Classes

Our observations revealed that Goliath Frogs partition microhabitats by age-class. Therefore, a range of different riverine habitat features is likely crucial for supporting the full complement of life stages of this species. Large adults predominately perched on rocks around waterfalls and rapids, with individual separated by a considerable distance (minimum 3–5 m), thereby providing evidence for territorialism and site fidelity, as already suggested by Sabater-Pi (1985). In contrast, subadults were rarely found around waterfalls. They appeared frequently on exposed, mid-stream rocks in the vicinity of cascades and waterfalls. Finally, metamorphosing and juvenile frogs most often used rook pools along the riverbeds where the current was slower. There they could find refuge in rock crevices when disturbed (Fig. 3C). Such sections also comprise the breeding sites of the species (Sabater-Pi 1985; Schäfer et al. 2019). The reason for this microhabitat partitioning is unclear. It may be a linked to thermoregulation, with small juveniles avoiding colder water, and/or predation pressure, including cannibalism. Habitat segregation has been reported from juvenile/subadult and adult European water frogs, *Pelophylax* spp., in order to escape cannibalism (Günther 1990).

Based on daytime observations, Sabater-Pi (1985) estimated the territory sizes of 20 to 40 m^2 for Goliath Frogs along the Mbia River. Our observations suggest that Goliath Frogs use small core areas or territories for sun-basking and shelter (200 m^2), and larger areas (> 1,000 m^2) for foraging. However, quantitative research on this issue is lacking and ideally should be based on radio-tracked individuals (e.g., Spieler 1997).

One surprising finding of this study was that the Goliath Frogs showed no apparent impact from the contamination with agrochemicals from neighboring plantations (at least to the extent that it is represented in our study sites; although, unfortunately, the composition and quantity of agrochemical run-off in the streams is unknown). On the Mpoula River, a large banana plantation that is

regularly sprayed by airplane occurs just upstream from where the Goliath Frogs were observed. In most of the study areas, small to medium-sized plantations along the rivers are run by local farmers. They typically use small spraying pumps and regularly process chemicals in the rivers, and the Goliath Frogs could still be found at these sites. Our observations, as well as the information from the frog hunters, revealed that populations around human settlements are smaller and adult frogs are rarer. As habitat degradation seemed to be of little influence, the Goliath Frogs might be mainly impacted by targeted hunting for food (locally) and trade.

Conservation Needs of the Goliath Frog

In order to detect potential declines, populations should be monitored on a regularly basis. However, no national monitoring program for Goliath Frog populations has been implemented thus far. Long-term data collection from specific sites across the Goliath Frog range would be essential for detecting changes in the distribution and local abundances of this species. Standard guidelines and techniques for monitoring amphibian populations and habitats are well-established (e.g., Heyer et al. 1994). Potential monitoring methods for Goliath Frogs should include time-area constrained searches in order to establish baseline data against which population changes with time could be judged. The data presented here may serve as a baseline for future studies. Based on our findings, regular surveys carried out at night by walking along pre-defined river routes would probably be the most efficient method. The Nkongsamba area is especially critical for monitoring because of the particularly intensive frog collection for food, and the severe habitat degradation overall. The Campo-Ma'an National Park and the Ebo Forest National Park should likewise be considered for monitoring, as they consist of areas with limited human impact. Monitoring in different parts of the species range will allow comparisons of the population trends within and outside protected areas. This will also potentially allow differentiation between the different threats such as collection, habitat degradation and pollution, climate change, and disease. Given that most amphibian populations naturally fluctuate (Pechmann et al. 1991), it would be ideal to start an initial monitoring program for at least five years.

Several key aspects of Goliath Frog ecology remain to be investigated in order to better understand the biology of this species (i.e., larval and juvenile survival rates, growth rates, age at maturity, and the longevity of adults). Such information may ultimately help in setting up a conservation action and management plan for this species. In parallel, additional short-term surveys (detecting as many populations as possible) and long-term monitoring data (to follow population trends) are needed to fully interpret the Goliath Frog's occurrences and threat status. This study has shown that conservation efforts for the Goliath Frog do not need to be prioritized for terrestrial habitat loss, but that hunting is clearly a prominent factor affecting the persistence of robust populations.

Acknowledgements.—We are very grateful to the many people and organizations who made this work possible. We are particularly grateful to Frogs & Friends e.V., Germany. The Cameroonian Ministry of Forestry and Wildlife (MINFOF) provided permission for the study. Our thanks are also extended to several organizations which commissioned part of the study (Rainbow Consult, Sylvatrop Consult, and Diggi Wels), and permitted the use of the data. We would also like to thank the local communities for permission to access their land. The people whose assistance in the field was invaluable include: Ekane Pierre, Andre, Blaise, Motto, Alex from the Nkongsamba region, Patrick, Olivier from Akom II and Blaise from around Ngo-Pem and Moukol, Ottou, and Nyanga boy and Black Joe from the Yabassi area. We thank the reviewers, in particular Thomas Doherty-Bone, for their constructive critiques on previous drafts of the manuscript.

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Amphibian & Reptile Conservation
16(2) [Taxonomic Section]: 120–132 (e320).

urn:lsid:zoobank.org:pub:7F752CB7-4667-46F5-A44E-E4D165D28CF4

Out of the Past: A new species of *Tantilla* of the *calamarina* group (Squamata: Colubridae) from southeastern coastal Guerrero, Mexico, with comments on relationships among members of the group

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***Abstract.*—A new species of *Tantilla* in the *calamarina* group from southeastern coastal Guerrero, Mexico is described. This new species is part of a clade that contains *T. calamarina*, *T. cascadae*, *T. ceboruca*, *T. coronadoi*, *T. deppei*, *T. sertula*, and *T. vermiformis*. All of these species are endemic to Mexico, except for *T. vermiformis*, which is found along the Pacific coastal plain from El Salvador to northwestern Costa Rica. Members of this group of *Tantilla* show varying adaptations to fossoriality, which might reflect their phylogenetic relationships.**

Keywords. *calamarina* group, centipede snake, fossoriality, phylogenetics, Reptilia, taxonomy

Resumen.— Describimos una nueva especie de *Tantilla* del grupo *calamarina* de la costa sureste de Guerrero, México. Esta nueva especie forma parte de un clado que contiene a *T. calamarina*, *T. cascadae*, *T. ceboruca*, *T. coronadoi*, *T. deppei*, *T. sertula* y *T. vermiformis*. Todas estas especies son endémicas de México, excepto *T. vermiformis*, que se encuentra a lo largo de la planicie costera del Pacífico desde El Salvador hasta el noroeste de Costa Rica. Los miembros de este grupo de *Tantilla* muestran diversas adaptaciones a la fosorialidad, lo que podría reflejar sus relaciones filogenéticas.

Palabras claves. Culebra ciempiés, fosorialidad, grupo *calamarina*, relaciones filogenéticas, Reptilia, taxonomía

Citation: Palacios-Aguilar R, Fucsko LA, Jiménez-Arcos VH, Wilson LD, Mata-Silva V. 2022. Out of the Past: A new species of *Tantilla* of the *calamarina* group (Squamata: Colubridae) from southeastern coastal Guerrero, Mexico, with comments on relationships within members of the group. *Amphibian & Reptile Conservation* 16(2) [Taxonomic Section]: 120–132 (e320).

Accepted: 11 October 2022; **Published:** 12 November 2022

Introduction

A recent paper by Palacios-Aguilar et al. (2021) noted a specimen of *Tantilla* from Guerrero that was collected over a century ago (BMNH 1906.6.1.241). This specimen, a female clearly referable to the *Tantilla calamarina* group (Wilson and Meyer 1981), was discussed by Wilson and Mata-Silva (2014) and determined to be either an atypical individual of *Tantilla coronadoi* or a representative of an unnamed taxon. Palacios-Aguilar et al. (2021) suspected the latter alternative because the three hitherto known specimens of *T. coronadoi* are consistent in key aspects of their scutellation, but they also declined to name a new species based on specimen BMNH 1906.6.1.241, which was collected in 1904 by Hans Gadow and reported as *Homalocranium miniatum* in his 1905 paper. According to Dixon et al. (2000), the name *H. miniatum* is a synonym of *T. rubra*.

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When the Palacios-Aguilar et al. (2021) paper appeared, one author of this paper (LDW) contacted the senior author and proposed reexamining the BMNH specimen to determine whether its status could be established more definitively, based on a modern understanding of the content and relationships within the *Tantilla calamarina* group. Consequently, the authors of this paper decided to collaborate in an attempt to determine on the status of this curious specimen, which has been lying in anonymity since it was collected 118 years ago.

The first four words of the title of this paper (Out of the Past) are used in reference to the period of time this specimen, which now becomes the holotype of a new species of *Tantilla*, has resided in the BMNH collection. These words also refer to the period of time that has elapsed since the person after whom this snake is being named began her journey in 1956 to find freedom from the tyranny in her homeland in her adopted land of Australia. For aficionados of cinema, *Out of the Past* will be recognized as the title of a well-regarded film noir, the 1947 work of French director Jacques Tourneur starring Robert Mitchum, Jane Greer, and Kirk Douglas.

Materials and Methods

During the last five decades, author LDW has been examining specimens of the genus *Tantilla*, resulting in the publication of several taxonomic treatments and species descriptions within this genus (e.g., Wilson and Meyer 1981; Wilson 1999; Wilson and Campbell 2000; Wilson and Mata-Silva 2014, 2015). While compiling information for the first taxonomic study of the *T. calamarina* species group (Wilson and Meyer 1981), measurements and scale counts were obtained for the specimen that now is the focus of this paper (BMNH 1906.6.1.241). Soon after that work started, the Senior Curator of Reptiles at the Natural History Museum, London, was contacted to obtain morphological data on the specimen, as well as high quality photographs. The photographs aided in making comparisons with the representatives of the *T. calamarina* species group.

In addition to the aforementioned works on the genus *Tantilla*, the comparisons in this paper benefitted from examinations of more recent literature specifically involving the *calamarina* species group (Canseco-Márquez et al. 2007; Cisneros-Bernal et al. 2020; Cruz-Sáenz et al. 2015; Dávalos-Martínez et al. 2021; Palacios-Aguilar et al. 2021; Ramírez-Bautista et al. 2014; Rocha et al. 2016), as well from the examination of comparative material housed at the Colección Nacional de Anfibios y Reptiles (CNAR) and the Museo de Zoología "Alfonso L. Herrera," Facultad de Ciencias (MZFC), both at the Universidad Nacional Autónoma de México. Scale counts and digital photographs of specimens deposited in the herpetological collection of the University of Texas at Arlington (UTA-R) were also obtained. The measurements are indicated in millimeters, and the ventral scales were counted following the method proposed by Dowling (1951), with the segmental counts referring to the sum of the ventrals + subcaudals, excluding the cloacal scute.

Results

After detailed comparisons of the BMNH specimen with the pertinent published sources and specimens held in scientific collections, we determined that BMNH 1906.6.1.241 does indeed represent a new species of the genus *Tantilla*.

Tantilla carolina, new species

Figs. 1–2.

Suggested common name. Carolina's Little Snake.

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Holotype. BMNH 1906.6.1.241, an apparent subadult or juvenile female from Tezonapan (= Tecoanapa), north of Ayutla, Guerrero, Mexico, collected by Hans Gadow in 1904.

Diagnosis. *Tantilla carolina* is a member of the *T. calamarina* group (Table 1). This species differs from *Tantilla calamarina* by the presence of more ventrals in females (156 versus [hereinafter = vs.] 118–140), more total segmental scales (194 vs. 146–179), a normally-sized preocular scale in contact with the postnasal scale (vs. a preocular with a tendency toward a decrease in size to complete the loss of the scale), two postocular scales (vs. one), seven supralabials (vs. usually six), a uniform dorsal head color followed by two pale postparietal spots (vs. a head pattern consisting of a spatulate dark anterior extension of the middorsal dark stripe flanked by

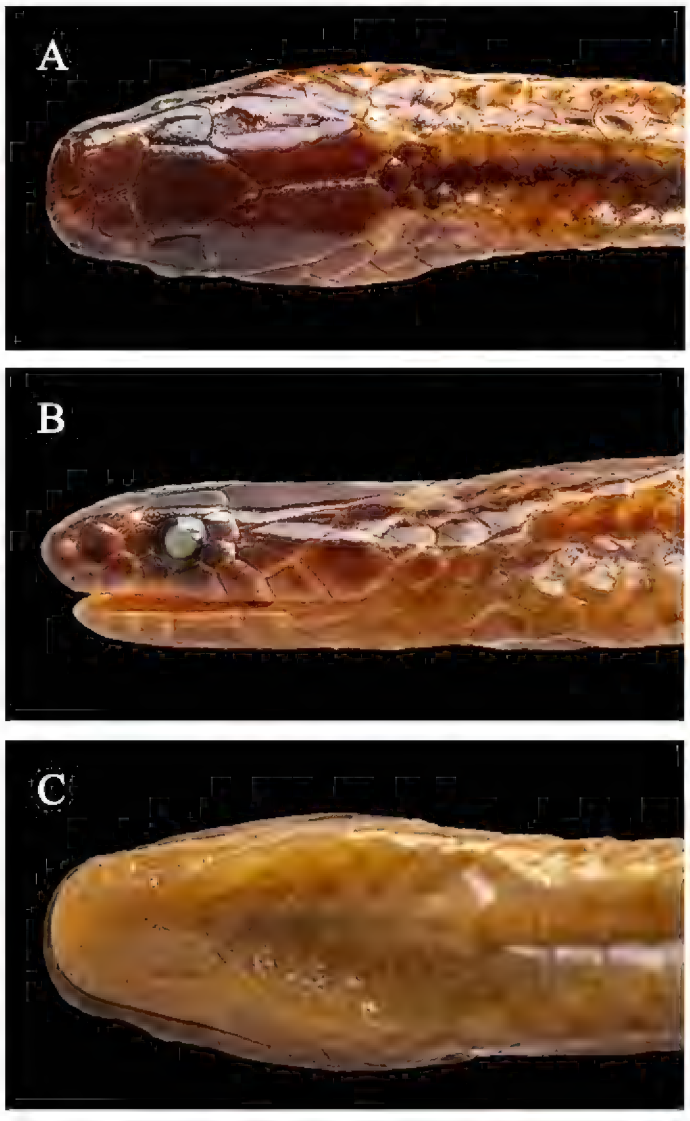

Fig. 1. Dorsal **(A)**, lateral **(B)**, and ventral **(C)** views of the head of the holotype of *Tantilla carolina* **sp. nov.** (BMNH 1906.6.1.241).

Fig. 2. Dorsal view of the holotype of *Tantilla carolina* **sp. nov.** (BMNH 1906.6.1.241).

prominent pale narrow longitudinal markings confluent with the pale postparietal spots), and a body pattern involving a dark lateral stripe that does not extend to the end of the body (vs. a dark brown lateral stripe on rows 3 and 4 extending the length of the body). The new species differs from *Tantilla cascadae* by the presence of more ventrals in females (156 vs. 139–144), more total segmental scales (194 vs. 176–192), seven supralabial scales (vs. six), and the dorsum of the head without a pattern but containing a pair of small pale postparietal spots (vs. a spatulate dark anterior extension of the middorsal dark stripe flanked by pale narrow longitudinal markings confluent with pale postparietal spots, or narrowly separated from the pale postparietal spots). The new species differs from *Tantilla ceboruca* by lacking a pattern and a pair of small pale postparietal scales on the dorsum of the head (vs. a spatulate extension of the middorsal dark stripe flanked by pale longitudinal markings confluent with postparietal spots and extending anteriorly along the sides of the parietal scales and across the supraoculars and prefrontals to join on the internasals), and a lateral portion of the head without a pattern (vs. one having each supralabial with a white border). The new species differs from *Tantilla coronadoi* by the presence of fewer ventral scales (156 vs. 165–178), fewer subcaudal scales (38 vs. 40–41), fewer total segmental scales (194 vs. 205–219), the anterior and posterior temporals in contact with one another (vs. those two scales separated from one another by contact of the 7th supralabial and the parietal scale), and the dorsal and lateral portions of the head lacking a pattern (vs. a dorsal head pattern consisting of a spatulate dark anterior extension of the middorsal dark stripe flanked by pale anterior extensions of the dorsolateral ground color, and a lateral head pattern consisting of supralabials with dark upper and pale lower portions). The new species differs from *Tantilla deppei* by the presence of fewer subcaudal scales (38 vs. 43–50), fewer total segmental scales (194 vs. 196–214), and the dorsal and lateral portions of the head lack a pattern and a pair of small pale postparietal spots (vs. a spatulate dark anterior extension of the middorsal dark stripe flanked by pale anterior extensions of a middorsally-divided pale nuchal band). The new species differs from *Tantilla sertula* by the presence of fewer ventrals in females (156 vs.161), more subcaudals in females (38 vs. 30), more total segmental scales (194 vs. 191), and the dorsal and lateral portions of the head lack a pattern (vs. a dorsal head pattern consisting of a spatulate dark anterior extension of the middorsal dark stripe flanked by prominent pale, narrow, longitudinal markings confluent with pale postparietal spots). The new species differs from *Tantilla vermiformis* by the presence of more ventral scales in females (156 vs. 120–129), more subcaudal scales (38 vs. 19–24), more total segmental scales (194 vs. 140–150), as well as by the presence of a small pair of pale postparietal spots confined to single scales (vs. a single pale spot crossing both parietal scales).

Description of the holotype (Figs. 1–2). An apparent subadult or juvenile female with 15 smooth dorsal scales throughout the trunk, 156 ventrals, a divided cloacal scute (= anal plate), 38 subcaudals, a total length of 112 mm, a tail length of 14 mm, and a tail/total length ratio of 0.125.

Nasal completely divided, posterior section in broad contact with a single preocular on both sides of head; two postoculars, approximately subequal in size; one anterior and one posterior temporal, in contact with one another, anterior temporal separating supralabials five, six, and seven from parietal, posterior temporal shorter than anterior temporal, approximately the shape of a dorsal body scale, although somewhat larger; supralabials 7–7, the 1st in contact with rostral, prenasal, postnasal, and 2nd supralabial, the 2nd with postnasal, preocular, and 3rd supralabial, the 3rd with preocular, orbit, and 4th supralabial, the 4th with orbit, lower postocular, and 5th supralabial, the 5th with lower postocular, anterior temporal, and 6th supralabial, the 6th with 5th supralabial, anterior temporal, and 7th supralabial, the 7th with the 6th

Table 1. Comparison of selected morphological features among the eight members of the *Tantilla calamarina* group. Data summarized from Wilson and Campbell (2000); Savage (2002); Canseco-Márquez et al. (2007); Wilson and Mata-Silva (2014); Cruz-Sáenz et al. (2015); Rocha et al. (2016); and Palacios-Aguilar et al. (2021).

Features	*T. carolina*	*T. calamarina*	*T. cascadae*	*T. ceboruca*	*T. coronadoi*	*T. deppei*	*T. sertula*	*T. vermiformis*
Total length (mm)	112	72–202	158–196	175–200	161–183	95–273	89–152	157
Tail length (mm)	14	13–36	30	33–35	25–31	16–62	12–21	—
Relative tail length	0.125	0.110–0.211	0.138–0.190	0.164–0.194	0.155–0.169	0.166–0.254	0.121–0.157	0.096–0.150
Ventrals in males	—	106–133 (119.7)	—	138–146	158	142–154 (145.9)	153?	115–123 (119.6)
Ventrals in females	156	118–140 (129.0)	139–144 (141.5)	153–178	165–178 (171.5)	148–168 (160.1)	160–161	120–129 (124.2)
Subcaudals in males	—	30–43 (36.8)	—	42–47	35+ (?)	54–62 (57.2)	37?	23–28 (25.3)
Subcaudals in females	38	22–43 (28.8)	37–48 (42.5)	36–41	40–41 (40.5)	43–58 (46.2)	30–33	19–24 (21.0)
Ventrals + subcaudals in males	—	145–166 (156.9)	—	180–193	—	196–213 (203.1)	190?	141–147 (144.5)
Ventrals + subcaudals in females	194	146–179 (158.0)	176–192 (184.0)	189–219	205–219 (212.0)	196–214 (206.3)	191–193	140–150 (144.7)
Preocular	Present, in contact with postnasal	Tendency toward decrease in size to complete loss	Present, in contact with postnasal	Present, in contact with postnasal or not	Present, in contact with postnasal	Present, in contact with postnasal	Present, in contact with postnasal	Present, in contact with postnasal, sometimes fused with prefrontal
Number of postoculars	2	1	2	2	2	2	2	2
Number of supralabials (number entering orbit)	7 (3+4)	Usually 6 (3+4)	6 (3+4)	7 (3+4)	7 (3–4)	Usually 7	6–7	7

Table 1 Continued. Comparison of selected morphological features among the eight members of the *Tantilla calamarina* group. Data summarized from Wilson and Campbell (2000); Savage (2002); Canseco-Márquez et al. (2007); Wilson and Mata-Silva (2014); Cruz-Sáenz et al. (2015); Rocha et al. (2016); and Palacios-Aguilar et al. (2021).

Features	*T. carolina*	*T. calamarina*	*T. cascadae*	*T. ceboruca*	*T. coronadoi*	*T. deppei*	*T. sertula*	*T. vermiformis*
Anterior and posterior temporals separated	No	No	No	No	Yes	No	No	No
Fusion of anterior temporals and sixth supralabial	No	No	No	No	No	No	No	Occasionally
Dorsal head pattern	Dorsum of head without pattern; pale postparietal spots limited to single scale located posterior to juncture between posterior temporal scale and parietal scale	Spatulate dark anterior extension of middorsal dark stripe flanked by prominent pale narrow longitudinal markings confluent with pale postparietal spots	Spatulate dark anterior extension of middorsal dark stripe flanked by pale narrow longitudinal markings confluent with pale postparietal spots or narrowly separated from postparietal spots	Spatulate extension of middorsal dark stripe flanked by pale longitudinal markings confluent with pale postparietal spots, and extending anteriorly along sides of parietals, and across supraoculars and prefrontals to join on internasals	Spatulate dark anterior extension of middorsal dark stripe flanked by pale anterior extensions of dorsolateral ground color	Spatulate dark anterior extension of middorsal dark stripe flanked by pale anterior extensions of middorsally-divided pale nuchal band	Spatulate dark anterior extension of middorsal dark stripe flanked by prominent pale narrow longitudinal markings confluent with pale postparietal spots	Dark brown dorsally and laterally with tan, pale lavender, or pale brown blotches on posterior portion of parietals
Lateral head pattern	Uniform in color	—	—	Each supralabial scale with a white border	—	—	Uniformly dark brown in color	—
Body pattern	Dark lateral stripe does not extend to end of body	Tan to brown with variously-sized dark middorsal stripe and a dark brown lateral stripe on rows 3 and 4	Pale brown with dark middorsal stripe occupying middle of middorsal scale row; dark lateral stripe on rows 3 and 4 only in neck region	Dark brown with dark middorsal stripe covering middle of middorsal scale row on most of body; dark lateral stripe on adjacent halves of rows 3 and 4	Tan to brown with dark middorsal stripe occupying middle of middorsal scale row and dark lateral stripe on rows 3 and 4	Tan to brown with diffused dark variously-sized middorsal stripe and dark lateral stripe on row 3 or rows 2 and 3; diffuse dark stripe on row 5	Dorsum pale brown on rows 5 to 7, dark brown on rows 1 to 4; dark middorsal stripe on middle of middorsal row, narrowing to series of disjunct longitudinal dashes continuing to end of tail	Pale brown to brown dorsum with poorly-defined, disjunct dark middorsal stripe confined to middorsal row
Ventral pattern	Immaculate cream	Immaculate cream	Cream to pale greenish yellow, with slight amount of dark pigment at lateral apices	Immaculate cream to pale greenish yellow	Immaculate cream to white	Immaculate cream	Immaculate cream	Immaculate white, cream, pale yellow, or pale pink

supralabial, anterior and posterior temporals, and two post-cephalic scales, with the 7th the largest; infralabials 6–6, with the 1st pair separated by contact of mental and anterior chinshields, the first four in contact with anterior chin shields, with the 4th largest; and anterior chinshields larger than posterior pair.

In preservative, the dorsal and lateral portions of the head are uniform dark brown, without a pattern (Fig. 1). A pair of pale postparietal spots, pale yellow in color, are present on the single scales located at the juncture of the parietal and posterior temporal scales, one each on either side of the head (Fig. 1). The dorsal ground color in preservative is brown with a dark brown middorsal stripe confined to the middorsal scale row, which extends to the end of the tail, breaking up into isolated dark spots, one per scale on the posterior region of the body and tail (Fig. 2). The remainder of the dorsum lacks a pattern. The venter is a uniform (perhaps cream) color in preservative.

Distribution. Known only from the type locality (Fig. 3). Tecoanapa is the seat of the municipality of Tecoanapa in the Pacific lowlands of southeastern Guerrero (coordinates 16°53'N, 99°24'W). Tecoanapa is a city located on Mexico Highway 95, east-northeast of Acapulco and south-southeast of Chilpancingo. The town lies at an elevation of 431 m (http://PueblosAmerica.com; accessed 30 March 2022). The vegetation in the region consists of a mixture of tropical deciduous forest (*selva baja caducifolia*), oak forest (*bosque de encino*), and agricultural lands, according to the available maps (CONABIO 1999).

Conservation assessment. The Environmental Vulnerability Score (EVS) for *Tantilla carolina* can be calculated as 6 + 8 + 2 = 16, which places its score in the middle of the high vulnerability category, as explained by Wilson et al. (2013).

Etymology. We are privileged to name this small snake in honor of the Hungarian Freedom Fighter Karolina Laszló (Fig. 4), in recognition of her dedication to the maintenance of human rights for all peoples in the face of totalitarianism, beginning with the Hungarian Revolution in 1956. As a young woman, Karolina was forced to join the exodus of her country people, in the company of her new husband, a soldier, Ede Károly Fucskó, who bravely defied the Hungarian dictatorship, communism, and the invading Soviet army. Ede Károly Udvarhelyi was adopted at an early age, when his mother remarried and thus kept the surname Fucskó. As the couple roamed through several European countries, in search of a refuge from the terror of oppressive political regimes, they escaped to England before seeking asylum in Australia. Due to unforeseen circumstances, however, the family of

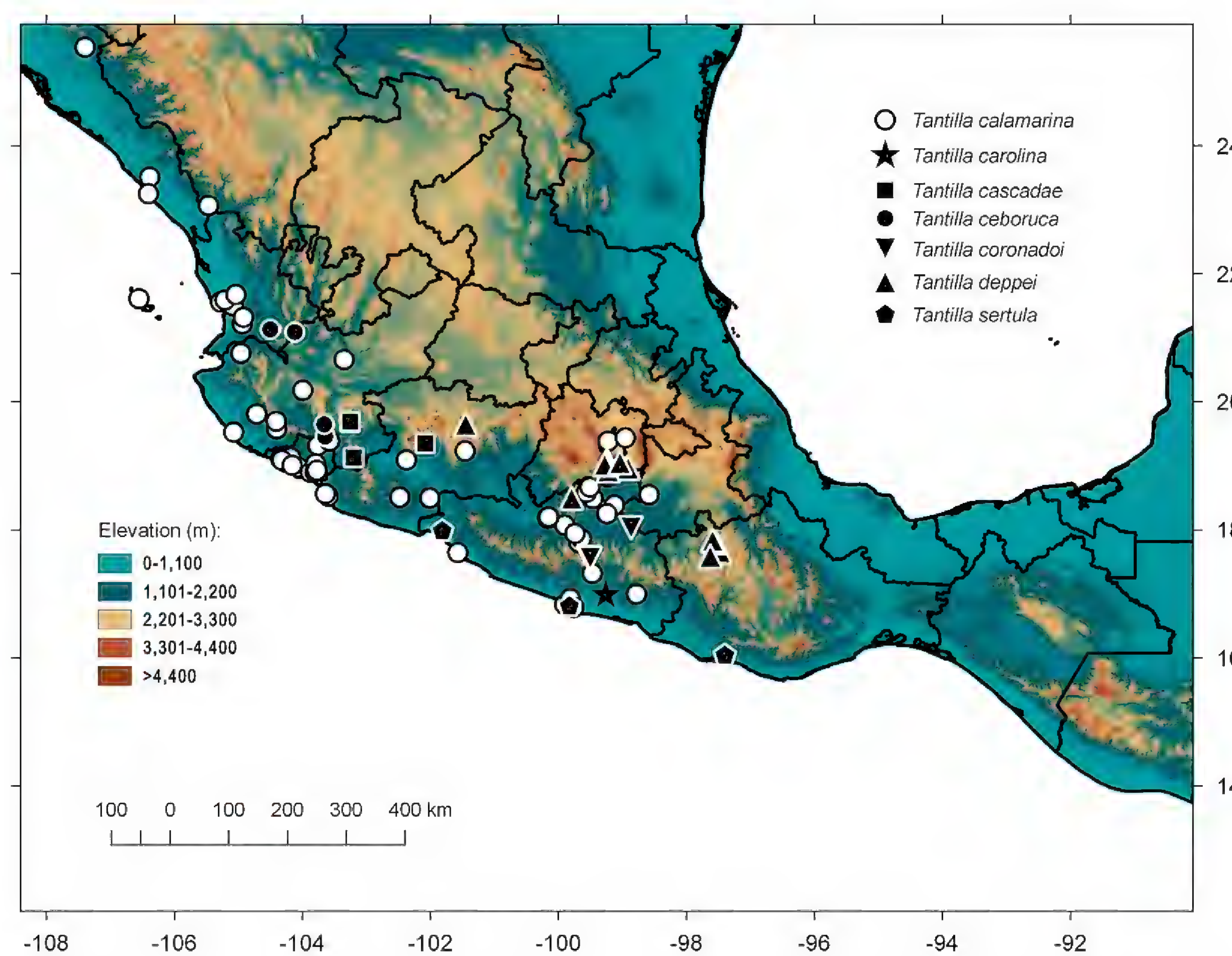

Fig. 3. Geographic distribution of the *Tantilla calamarina* group species in western Mexico. The black star represents the type locality of *Tantilla carolina* **sp. nov.** described herein.

Key to the members of the *Tantilla calamarina* group

1. Anterior and posterior temporals separated by contact of 7th supralabial and parietal. . . . . *T. coronadoi*
Anterior and posterior temporals in contact, not separated by contact of 7th supralabial and parietal 2

2. Postocular single . . . . *T. calamarina*
Postoculars two. 3

3. Ventrals fewer than 130; subcaudals fewer than 30 . . . . *T. vermiformis*
Ventrals 130 or more; subcaudals 30 or more 4

4. Ventrals 144 or fewer . . . . *T. cascadae*
Ventrals 153 or more 5

5. Dark lateral stripe present 6
Dark lateral stripe absent 7

6. Dark lateral stripe on adjacent halves of rows 3 and 4 . . . . *T. ceboruca*
Dark lateral stripe on row 3 or on rows 2 and 3 . . . . *T. deppei*

7. Dorsal head pattern consists of a spatulate dark anterior extension of the middorsal dark stripe occupying dorsum of head, flanked by pale, narrow, longitudinal stripes broadly separated from pale postparietal spots occupying portions of three dorsal scales immediately posterior to the posterolateral portion of each parietal scale. . . . . *T. sertula*
Dorsum of head without pattern, uniform brown in color; pale postparietal spots each confined to single postparietal scales . . . . *T. carolina* **sp. nov.**

five later travelled back to Hungary, residing there for several years before escaping again to Vienna, Austria, then travelling to Italy, and from there they journeyed to South Africa. There, they dared to oppose the policy of apartheid but eventually, under duress, had to flee as interracial tensions escalated into further hostilities and reprisals. Finally, the family found relative solace in the democratic land of Australia, where life remained challenging in such a strangely beautiful land. During this long trek to find a life of freedom, Karolina and Ede were accompanied by their three children, John Edward, Stephen Charles, and a co-author of this paper, Lydia Allison Fucsko. Therefore, in Karolina's honor, we named this snake *Tantilla carolina* **sp. nov.**, with a reference to the meaning of the name Carolina in Spanish as "the prettiest woman of the town," an apt descriptor for this truly lovely, indomitable, and spirited lady whose humanitarian efforts continue to inspire future generations.

Discussion

Wilson and Meyer (1981: 2–3) established a case for the recognition of the *Tantilla calamarina* group, which they maintained consisted of four species, including *T. calamarina*, *T. coronadoi*, *T. deppei*, and a species they described as new, *T. cascadae*. The justification for their recognition of the *calamarina* group primarily was based on a "similarity in head pattern." Wilson and Meyer (1981: 2) detailed that all four species they recognized as part of this group "have the central portion of the parietals covered with a spatulate anterior extension of the middorsal dark stripe, which continues anteriorly to cover the remainder of the head. On either side of this central head mark is a postparietal pale spot that usually grades posteriorly into the ground color of the dorsolateral field [...] and, in its best-developed state, connects

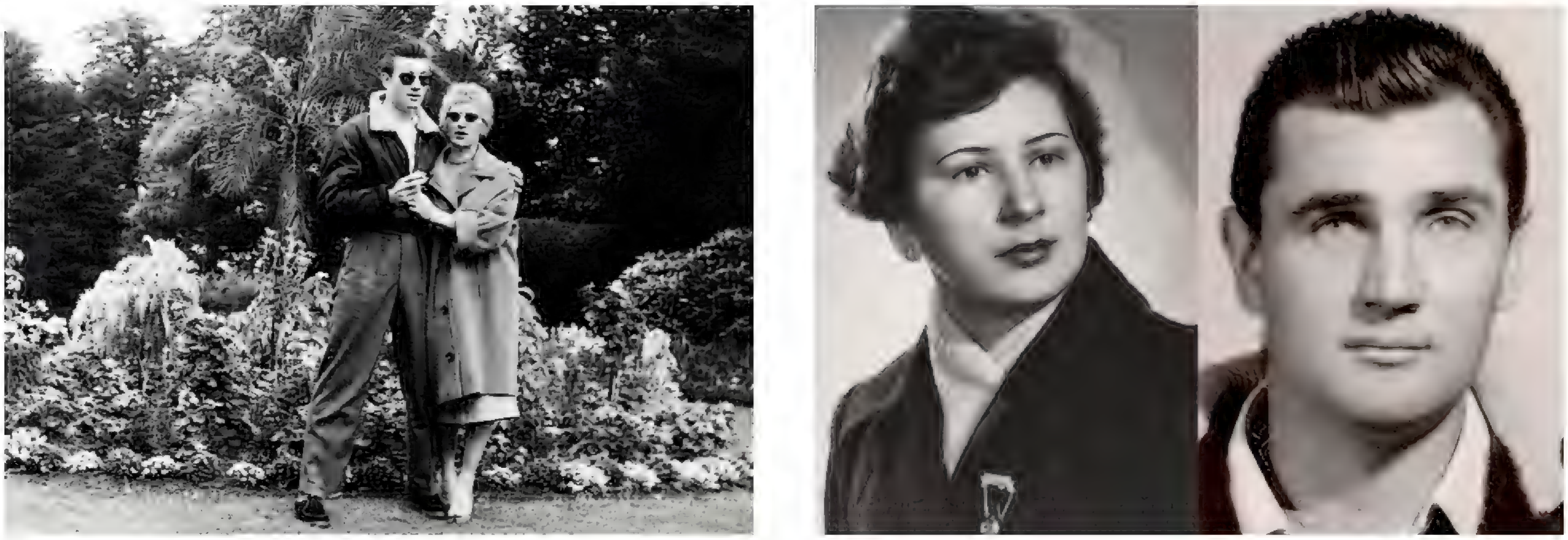

Fig. 4. (Left) The Hungarian Freedom Fighters, Karolina and Ede Károly Fucskó, in Hyde Park, London, England, 1958. (Right) Enduring photographs of Karolina and Ede Károly Fucskó.

anteriorly with a narrow extension that proceeds along the side of the parietal, over the supraocular and onto the side of the prefrontals and internasals." The members of this group also exhibit a dark middorsal stripe occupying some portion of the middorsal scale row and, in some cases, a portion of the adjacent dorsal scale rows.

In subsequent years, another species of *Tantilla*, *T. vermiformis*, was allocated to the *calamarina* group (Wilson 1999). This allocation, however, was questioned by Holm (2008: 98), who stated that "[his] results [lead him] to not include *T. vermiformis* in the *T. calamarina* group as suggested by Wilson et al. (1999) and Wilson and Campbell (2000). Similarities between these taxa may be due to convergent adaptations for fossoriality and the dark vertebral line is a shared primitive trait." Other hypotheses worth testing when sufficient molecular material becomes available would include whether *T. vermiformis* is more closely related to the members of the *T. melanocephala* group (Wilson and Mena 1980) or to some other member or members of the genus not yet identified.

In 2000, Wilson and Campbell described *Tantilla sertula* based on a single specimen from Pacific coastal Guerrero, Mexico, and allocated this species to the *calamarina* group. A second specimen of this species was documented from the coastal plain of Guerrero by Canseco-Márquez et al. (2007). Thereafter, Rocha et al. (2016) reported a third specimen of this species from the lower foothills of the Sierra Madre del Sur of southern Oaxaca. Finally, Canseco-Márquez et al. (2007) described *Tantilla ceboruca* from southern Nayarit, Mexico. These authors also placed this species in the *calamarina* group.

Thus, with the description of *T. ceboruca* in 2007, the *calamarina* group was considered to consist of seven species, including, in order of year of description: *T. vermiformis* (Hallowell 1861), *T. calamarina* (Cope 1866), *T. deppei* (Bocourt 1883), *T. coronadoi* (Hartweg 1944), *T. cascadae* (Wilson and Meyer 1981), *T. sertula* (Wilson and Campbell 2000), and *T. ceboruca* (Canseco-Márquez et al. 2007). With the description of *T. carolina*, the genus *Tantilla* currently is known to contain 68 species (The Reptile Database, http://www.reptile-database.org/; accessed 15 May 2022).

Most species in the *calamarina* group are distributed in the western portion of Mexico, from northern Sinaloa to south-central Oaxaca, except for *Tantilla vermiformis*, which is found along the Pacific coastal plain of Central America from El Salvador to northwestern Costa Rica (Wilson and Mata-Silva 2015; Antúnez-Fonseca et al. 2020a). The northernmost-occurring and most widely-distributed species in the group is *T. calamarina*, which is known from northern Sinaloa to south-central Guerrero, including the Tres Marías Islands (Isla María Madre) lying off Nayarit; the elevational range for this species is from near sea level to 1,677 m asl. In comparison, the remaining species in the group are narrowly distributed, as follows: *T. cascadae* (1,430–1,858 m asl from south-central Jalisco to central Michoacán); *T. ceboruca* (1,233–2,094 m asl from southeastern Nayarit to north-central Jalisco); *T. coronadoi* (650–1,524 m asl in northeastern and central Guerrero); *T. deppei* (1,524–2,438 m asl in northern Morelos, northern Guerrero, and northwestern Oaxaca); *T. sertula* (near sea level–487 m asl from northwestern Guerrero to south-central Oaxaca); and *T. vermiformis* (40–520 m asl from El Salvador to northwestern Costa Rica).

One of the most obvious features of the species presently allocated to the *calamarina* group is that they show varying adaptations to a fossorial existence. Ramírez-Bautista et al. (2014) developed a so-called "index of fossoriality" to quantify the degree of fossorial adaptation among the seven members of this group, as then comprised, based on features of cephalic scutellation and segmental counts. These features were documented in Table 1 of that paper, converted to character states that were placed in Table 2 of that paper, which then were collated to produce an index of fossoriality. The reader should refer to that paper for a more thorough explanation of the index of fossoriality. These authors concluded their analysis of fossoriality in the *calamarina* group by stating (pp. 803–804) that "low indices [of fossoriality] are found in the more generalized *calamarina* group species, such as *T. sertula* and *T. deppei*…, intermediate values are found in the more adapted species, such as *T. ceboruca*, *T. coronadoi*, *T. cascadae*, and *T. vermiformis*…, and high indices in the most adapted species, i.e., *T. calamarina* and *G. redimitus*."

Using the methodology employed by Ramírez-Bautista et al. (2014), we determined the index of fossoriality for *Tantilla carolina* as follows:

Preocular present—1
Preocular in contact with postnasal—1
Preocular fused with prefrontal and supraocular—1
Number of postoculars—1
5th supralabial separated from parietal—1
6th supralabial fused with anterior temporal—1
7th supralabial and parietal in contact—1
Number of supralabials—1
Supralabials entering orbit—1
Number of ventrals—1
Number of subcaudals—2

The sum of these 11 character-values for *T. carolina* is 12, the same value as calculated for *T. sertula* by Ramírez-Bautista et al. (2014). This index of fossoriality is the lowest among the members of the *calamarina* group, in which the indices range from 12 to 24 (including that for *Geagras redimitus*, which was included in the *calamarina* group by Holm [2008]). This determination indicates that *T. carolina* and *T. sertula* are the two members of the group that are the least adapted for a fossorial existence. The indices of fossoriality for the other species involved, in increasing value, are as follows: *T. deppei* (13); *T. ceboruca* and *T. coronadoi* (both 14); *T. cascadae* (15); *T. vermiformis* (16); *T. calamarina* (21); and *G. redimitus* (24).

As noted by Ramírez-Bautista et al. (2014), the index of fossoriality is not intended to elucidate the phylogenetic relationships within the *calamarina* group, but it is tempting to hypothesize that this index perhaps is reflective of the phylogenetic relationships that could

be substantiated by a molecular analysis, should such an analysis ever become possible. The timeline for such an analysis is difficult to predict, especially because most of the species involved are known from only a handful of preserved specimens (or only one).

If and when a molecular analysis of the phylogenetic relationships of this group of snakes becomes possible, five questions of principal interest to answer would be the following: (1) Is *Geagras redimitus* closely related enough to the members of the *Tantilla calamarina* group to be subsumed into this group, as per the conclusion of Holm (2008)? (2) Is *Tantilla vermiformis* closely related enough to the unquestioned members of the *calamarina* group to be included within it, or do its closest relationships lie elsewhere in the genus *Tantilla*? (3) Is *Tantilla carolina* closely related enough to the unquestioned members of the *calamarina* group to be included within it? (4) What are the phylogenetic relationships of the nine species involved to one another? and (5) What are the relationships of these species to the other members of the genus *Tantilla*?

In their treatment of the *Tantilla* clade, Wilson and Mata-Silva (2015) noted that the genus *Tantilla* contained 61 species at that point. With the description of *Tantilla carolina*, the genus now contains 68 species, and it remains the second largest genus of snakes in the Western Hemisphere after *Atractus* (currently containing 146 species, according to The Reptile Database, http://www.reptile-database.org/; accessed 9 April 2022). Only one other snake genus contains more species than *Tantilla*, the Old-World genus *Oligodon* (presently consisting of 88 species, according to The Reptile Database, http://www.reptile-database.org/; accessed 9 April 2022). The seven species of *Tantilla* described since the Wilson and Mata-Silva (2015) paper was published are (listed alphabetically): *T. berguidoi* Batista et al. 2016; *T. excelsa* McCranie and Smith 2017; *T. gottei* McCranie and Smith 2017; *T. lydia* Antúnez-Fonseca et al. 2020b; *T. stenigrammi* McCranie and Smith 2017; and *T. tjiasmantoi* Koch and Venegas 2016. Six of these seven species are allocated to the *Tantilla taeniata* group. The remaining species (*T. tjiasmantoi*) was not placed in a species group by the original authors, but its unusual pattern of dark banding on a pale ground color might suggest that this species is allied with another South American species that sometimes is banded, *T. semicincta* (Wilson 1976).

In the last two decades, about 40 new species of snakes have been described from Mexico, including four that are known to occur on the Pacific Coastal Plains (PCP), where the holotype of *T. carolina* was obtained (i.e., *Tantilla sertula* Wilson and Campbell 2000; *Thamnophis rossmani* Conant 2000; *Coniophanes michoacanensis* Flores-Villela and Smith 2010; and *Rhadinella dysmica* Campillo et al. 2016). Surprisingly, this region has received less attention when compared with the adjacent elevations of the Sierra Madre del Sur, and few collections have been made in this area (e.g., Holman 1964; Liner and Dundee 1969; Saldaña de La Riva and Pérez Ramos 1987; Schätti and Stutz 2016). Recent scattered reports have recorded several species of snakes with hitherto restricted ranges that were found hundreds of kilometers from their previously known localities (Siria-Hernández et al. 2006; Rocha et al. 2016; Blancas-Hernández et al. 2019; Arrazola-Bohórquez and Palacios-Aguilar 2022), which apparently reinforces the proposal of Flores-Villela and Goyenechea (2001) that this province serves both as a corridor for lowland species and as a barrier for montane species of amphibians and reptiles. Nonetheless, there are areas of the PCP where interesting sets of microendemic species of reptiles are found (Palacios-Aguilar et al. 2018), and overall, a high proportion of endemic amphibians and reptiles occur in this province (Johnson et al. 2017), which might suggest that it is not as homogeneous as previously considered and that biotic subprovinces may be present within it. Detailed, objective biogeographic studies are necessary to test this hypothesis, now that novel information on species previously known from few localities or specimens is emerging.

Incomplete information and sampling biases affect what we know about biodiversity. The biodiversity *shortfalls* such as the Wallacean, the limited knowledge on the distribution of species, and the Linnean, the proportion of undescribed diversity, are two of the most important limiting factors that beset our understanding and knowledge of the natural world (Hortal et al. 2015). The effect that roads have on the vertebrate fauna of southern Mexico has been reported (Bojórquez-Tapia et al. 1994, 1995), and it is expected to diminish progressively as collectors and researchers reach previously inaccessible regions. In recent decades, it has been reported that species extirpations and extinctions have been augmented in an unprecedented way due to the negative impact of human activities (Dirzo et al. 2014). This highlights the importance of having accurate and reliable sources of biological information, such as scientific collections, that help us to diminish the effects of these shortfalls and allow us to provide an accurate image of how many, where, and which species exist in a particular region. Also, one should note that not all taxa have the same rate of species descriptions, and particularly in snakes, the *shelf-life* that specimens have from their collection to their description ranges from 0 to 146 years (mean 7.5 years, Guedes et al. 2020), inasmuch as the conduct of taxonomic treatments is one of the factors that boosts species discovery. The new species described herein has "awaited" being described for 118 years, which makes it a snake species with one of the longest shelf lives, and thanks to the conduct of a taxonomic treatment and the adequate housing of the individual in one of the world's largest scientific collections, it was possible to identify it as a novel taxon. We can only imagine how many more species in Mexico (and the world) probably are now on a shelf awaiting discovery.

Acknowledgments.—We are indebted especially to Patrick Campbell, who made it possible for us to obtain basic morphological data on the BMNH specimen we designated as the holotype of the new species of *Tantilla* described herein. We also wish to thank Louis W. Porras for assistance in securing the necessary literature for use in this paper, and for his masterful review of our work. We also are grateful to David Lazcano for his review, which greatly improved our manuscript. We also thank Marisol Gómez for her invaluable help in editing the figures. Luis F. Nieto Toscano, Gregory G. Pandelis (UTA), Victor H. Reynoso (CNAR), Oscar Flores-Villela, and Leticia M. Ochoa-Ochoa (MZFC) provided access, associated data, photographs, and measurements of the specimens under their care or those with which they were working.

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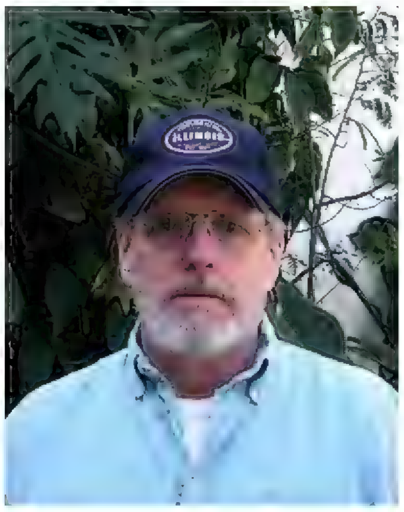
Lydia Allison Fucsko, who resides in Melbourne, Australia, is an environmental activist and amphibian conservationist. As a photographer with international publications, she has taken countless amphibian photographs, including photo galleries of frogs mostly from southeastern Australia. Lydia has a Bachelor of Humanities from La Trobe University (Bundoora, Victoria, Australia) and a Diploma in Education from the University of Melbourne (Parkville, Victoria, Australia). She has postgraduate diplomas in computer education and in vocational education and training from the University of Melbourne (Parkville). Additionally, Lydia has a Master's Degree in Counseling from Monash University (Clayton, Victoria, Australia). She received her Ph.D. on Environmental Education, in which she promoted habitat conservation, species perpetuation, and global sustainable management, from Swinburne University of Technology (Hawthorn, Victoria, Australia), while being mentored by the late Australian herpetologist and scholar Dr. Michael James Tyler (Order of Australia recipient). Lydia is a sought-after educational consultant, with academic interests that include: clinical psychology, focusing on psychopathology; neuroscience and empathy; environmental education for sustainable development; sentient ecology; academic writing; and creative writing, which includes poetry and creative non-fiction books for children and young adults. She also is the senior author (with Boria Sax) of a chapter in the 2019 *Springer Encyclopedia of Sustainability in Higher Education* entitled "Learning Activities for Environmental Education for Sustainable Development." Recently, Lydia has co-authored an obituary of Jaime D. Villa, a study of the introduced Mesoamerican herpetofauna, a treatment of conservation prospects of the Mesoamerican salamander fauna, papers on the herpetofauna of Veracruz and Querétaro, Mexico, a review of the book *Advances in Coralsnake Biology*, and a study on the biological and cultural diversity of Oaxaca, Mexico, among several other academic papers. In 2020, the species *Tantilla lydia*, with the suggested common name of Lydia's Little Snake, was named in her honor.

Víctor H. Jiménez Arcos is an Associate Professor and the head of the Herpetology Lab, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México. Through studies on ecology and evolutionary biology, his laboratory focuses on understanding the evolution of the phenotypic diversity of amphibians and reptiles, as well as the changes and losses of geographical range associated with anthropogenic factors. He also works intensively with human communities and the Mexican government agency in charge of Natural Protected Areas (CONANP) to achieve the conservation of amphibian and reptile species in the short, medium, and long term.



Larry David Wilson is a herpetologist with lengthy experience in Mesoamerica. He was born in Taylorville, Illinois, USA, and received his university education at the University of Illinois at Champaign-Urbana (B.S. degree) and at Louisiana State University in Baton Rouge (M.S. and Ph.D. degrees). He has authored or co-authored more than 465 peer-reviewed papers and books on herpetology. Larry is the senior editor of *Conservation of Mesoamerican Amphibians and Reptiles* and a co-author of seven of its chapters. His other books include *The Snakes of Honduras*, *Middle American Herpetology*, *The Amphibians of Honduras*, *Amphibians & Reptiles of the Bay Islands and Cayos Cochinos, Honduras*, *The Amphibians and Reptiles of the Honduran Mosquitia*, and *Guide to the Amphibians & Reptiles of Cusuco National Park, Honduras*. To date, he has authored or co-authored the descriptions of 75 currently recognized herpetofaunal species, and seven species have been named in his honor, including the anuran *Craugastor lauraster*, the lizard *Norops wilsoni*, and the snakes *Oxybelis wilsoni*, *Myriopholis wilsoni*, and *Cerrophidion wilsoni*, as well as the oligochaete annelid *Pheretima wilsoni* and the coccidian parasite *Caryospora wilsoni*. In 2005, he was designated a Distinguished Scholar in the Field of Herpetology at the Kendall Campus of Miami-Dade College. Currently, Larry is a Co-chair of the Taxonomic Board for the website *Mesoamerican Herpetology*.

Vicente Mata-Silva is a herpetologist originally from Río Grande, Oaxaca, Mexico. His interests include ecology, conservation, natural history, and biogeography of the herpetofaunas of Mexico, Central America, and the southwestern United States. He received a B.S. degree from the Universidad Nacional Autónoma de México (UNAM), and M.S. and Ph.D. degrees from the University of Texas at El Paso (UTEP). Vicente is an Assistant Professor of Biological Sciences at UTEP, in the Ecology and Evolutionary Biology Program, and Co-Director of UTEP's Indio Mountains Research Station, located in the Chihuahuan Desert of Trans-Pecos, Texas, USA. To date, Vicente has authored or co-authored over 100 peer-reviewed scientific publications. He also was the Distribution Notes Section Editor for the journal *Mesoamerican Herpetology*, and is currently Associate Editor for the journal *Herpetological Review*.

Appendix

Appendix I. In addition to published sources, the following comparative material was examined. All localities are in Mexico.

Tantilla calamarina. GUERRERO: Acapulco de Juárez, Viveros "El Huayacán," La Poza (CNAR 29208–220, MZFC 13810–815), Puerto Marquéz (CNAR 18729–735); Apaxtla de Castrejón, Tecolhuiztle (MZFC 2206); Arcelia, Campo Morado, Cañada El Limón (MZFC19793, 19798–801), Campo Morado, Cañada El Naranjo (MZFC 19795, 19797), Agua Zarca (MZFC 19794, 19796); Eduardo Neri, San Miguel, Rancho del "Patillas" (MZFC 35822, 35826); Pilcaya, Parque Nacional Grutas de Cacahuamilpa (CNAR 28923–924).

Tantilla ceboruca. JALISCO: Road between Copala and Ciudad Guzman, N of Nevado de Colima (UTA-R 58516).

Tantilla coronadoi. GUERRERO: Copalillo, 2.5 km NE Papalutla (MZFC 25507).

Tantilla deppii. OAXACA: 3.2 km SW of Yosocuno (MZFC 33820, 33822); San Pedro Nopala, Maguey Verde (MZFC 33747).

Introductory page. *Dryophytes eximius* (Baird, 1854). The distribution of the Mountain Treefrog extends from south-central Durango and the Sierra Madre Oriental in Tamaulipas southward to the Transverse Volcanic Range of Jalisco, Colima, Michoacán, México, Morelos, Distrito Federal, Puebla, Hidalgo, and Veracruz, Mexico (Frost 2022). This individual was photographed in the community of El Garbanzo, in the municipality of Irapuato. Wilson et al. (2013b) calculated its EVS as 10, placing it at the lower limit of the medium vulnerability category. IUCN has considered its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

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Amphibian & Reptile Conservation
16(2) [General Section]: 133–180 (e321).

The herpetofauna of Guanajuato, Mexico: composition, distribution, and conservation status

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***Abstract.*—The herpetofauna of the Mexican state of Guanajuato currently consists of 24 anurans, three salamanders, 71 squamates, and three turtles, for a total of 101 species. The members of the herpetofauna are categorized among the three recognized physiographic regions of the Central Plateau, the Transmexican Volcanic Belt, and the Sierra Madre Oriental. The total number of species in each of these regions ranges from 60 in the Central Plateau to 75 in the Sierra Madre Oriental. The numbers of species shared among these three regions range from 44 between the Central Plateau and the Sierra Madre Oriental to 56 between the Central Plateau and the Transmexican Volcanic Belt. A similarity dendrogram based on the Unweighted Pair Group Method with Arithmetic Averages (UPGMA) demonstrates that of the three physiographic regions, the Central Plateau (CP) and the Transmexican Volcanic Belt (TVB) cluster at the 0.84 level, and that the Sierra Madre Oriental (SMO) clusters with the other two regions at the 0.65 level. This pattern was expected given that both the CP and TVB are relatively large areas of similar size in the state that lie adjacent to one another; in contrast, the SMO is the smallest region in the state and it is adjoined only to the CP region. The level of herpetofaunal endemism in Guanajuato is relatively high, with 56 of the 101 species categorized as country endemics. The distributional categorization of the entire herpetofauna includes 56 country endemics, 40 non-endemics, and five non-natives. The 40 non-endemic species are placed into the following distributional categories: MXUS (26), USCA (six), MXCA (four), MXSA (three), and USSA (one). The principal environmental threats to the herpetofauna of Guanajuato are agriculture, industry, forestry, cattle production, and mining. We assessed the conservation status of each native species by using the SEMARNAT, IUCN, and EVS systems, of which the EVS system proved to be the most useful. We applied the Relative Herpetofaunal Priority method to determine the rank order of the three regions, which indicates that the Transmexican Volcanic Belt is the region of greatest conservation importance. Twenty-four natural protected areas have been designated in Guanajuato. Fourteen of these areas lie within the Transmexican Volcanic Belt, which is fortunate from a conservation perspective. All but four native species have been documented in these 24 areas. Finally, we provide a set of conclusions and recommendations to help improve the future protection of the Guanajuato herpetofauna.**

Keywords. Anurans, caudates, physiographic regions, protected areas, protection recommendations, squamates, turtles

***Resumen.*—La herpetofauna del estado mexicano de Guanajuato actualmente consiste de 24 anuros, tres salamandras, 71 escamosos y tres tortugas, para un total de 101 especies. Los miembros de la herpetofauna se clasifican en tres regiones fisiográficas reconocidas, que incluyen la Meseta Central, la Faja Volcánica Transmexicana y la Sierra Madre Oriental. El número total de especies en estas regiones consiste desde 60 en la Meseta Central hasta 75 en la Sierra Madre Oriental. El número de especies compartidas entre estas tres regiones va desde 44 entre el Altiplano Central y la Sierra Madre Oriental hasta 56 entre el Altiplano Central y la Faja Volcánica Transmexicana. Un dendrograma de similitud basado en el Método de Grupos de Pares No Ponderados con Promedios Aritméticos (UPGMA) demuestra que de las tres regiones fisiográficas, la Meseta Central (CP) y la Faja Volcánica Transmexicana (TVB) se agrupan en el nivel .84 y que la Sierra Madre Oriental (SMO) se agrupan con las otras dos regiones en el nivel .65. Se espera este patrón dado que CP y TVB son áreas relativamente grandes de tamaño similar en el estado y son adyacentes entre sí; de lo contrario, la**

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SMO es la región más pequeña del estado y está unida solo a la región CP. El nivel de endemismo de la herpetofauna en Guanajuato es relativamente alto, con 56 de las 101 especies categorizadas como endémicas del país. La categorización distribucional de toda la herpetofauna es la siguiente: 56 endémicas del país, 40 no endémicas y cinco no nativas. Las 40 especies no endémicas se ubican en las siguientes categorías de distribución: MXUS (26), USCA (seis), MXCA (cuatro), MXSA (tres) y USSA (una). Las principales amenazas ambientales son agricultura, industria, silvicultura, ganadería y minería. Evaluamos la conservación de cada especie nativa utilizando los sistemas de SEMARNAT, UICN y EVS, de los cuales el sistema EVS demostró ser el más utilitario. Se utilizó el método de Prioridad Relativa de la Herpetofauna para determinar el orden de clasificación de las tres regiones, y este método indicó que la Faja Volcánica Transmexicana es la región de mayor importancia para la conservación. Todas menos cuatro especies nativas están documentadas en estas 24 áreas. Finalmente, brindamos un conjunto de conclusiones y recomendaciones destinadas a aumentar las posibilidades para la futura protección de la herpetofauna guanajuatense.

Palabras Claves. Anuros, áreas protegidas, caudados, escamosos, estatus de conservación, recomendaciones de protección, regiones fisiográficas, tortugas

Citation: Leyte-Manrique A, Mata-Silva V, Báez-Montes O, Fucsko LA, DeSantis DL, García-Padilla E, Rocha A, Johnson JD, Porras LW, Wilson LD. 2022. The herpetofauna of Guanajuato, Mexico: composition, distribution, and conservation status. *Amphibian & Reptile Conservation* 16(2) [General Section: 133–180 (e321).

Accepted: 10 October 2022; **Published:** 30 November 2022

"If we keep trashing our unique ecosystems, how much longer with they be able to deal with wave after wave of new challenges?"

Rick Shine (2018)

Introduction

The state of Guanajuato is located in central Mexico, at the intersection of three major physiographic regions: the Central Plateau, the Transmexican Volcanic Belt, and the Sierra Madre Oriental. To the north, the state is bounded by a sliver of Zacatecas and a large portion San Luis Potosí, to the east by Querétaro, to the south by Michoacán, and to the west by Jalisco. Guanajuato is the 22nd largest state in Mexico, with a surface area of 30,607 km^2 (http://inegi.org.mx/monografias/informacion/gto/; Accessed 18 February 2022). In 2020, the population of the state was 6,166,934, which ranks sixth in the country, and the state's population density is 200 people/km^2, which ranks fifth (http://inegi.org.mx/monografias/informacion/gto/poblacion/default.aspx; Accessed 25 May 2022).

Historically, Guanajuato is an important place with regard to the Mexican herpetofauna, since this state is considered the birthplace for the formal study of these ectotherms by the father of Mexican herpetology, Alfredo Dugès, who conducted the first studies on the diversity of vertebrates, including aspects of their natural history (Reynoso et al. 2012; Leyte-Manrique et al. 2015; Flores-Villela et al. 2018). Dugés recorded 56 species in the state, including 12 amphibians and 44 reptiles. However, although Guanajuato has been important in the Mexican herpetological literature, there is no species list representing the current composition of its herpetofauna. In this regard, the study of Mendoza-Quijano et al. (2001), carried out in Sierra de Santa Rosa, is viewed as the watershed work for formally reestablishing the investigation of the herpetofauna found in this state. Important recent works include *Guía de los Anfibios y Reptiles de Charco Azul, Xichú, Guanajuato* (Leyte-Manrique and Domínguez-Laso 2014), which provides a list of 18 species. Subsequently, two studies in 2018 assessed the herpetofauna at a larger scale. Báez-Montes (2018) reported a total of 86 species (21 amphibians and 65 reptiles) living in natural protected areas, and Arciga-Hernández et al. (2018) reported 108 species (27 amphibians and 81 reptiles). The latter study was based mostly on records from natural protected areas, but it includes species present in the surrounding states that are also potentially found in Guanajuato. Furthermore, areas outside of the natural protected areas in Guanajuato, both considerably undisturbed and disturbed (such as agro-ecosystems), have been studied during the last six years (Cadena-Rico et al. 2020; Leyte-Manrique et al. 2015, 2016, 2019, 2021; Letye-Manrique 2022). The work of Leyte-Manrique et al. (2015) focused on the entire herpetofauna of the state, from both historical and contemporaneous perspectives, and discusses the findings in 10 published papers. Herein, we provide an updated assessment of the herpetofauna of Guanajuato.

Materials and Methods

Our Taxonomic Position

In this contribution we follow the taxonomic position that was explained in detail in previous works on other portions of Mesoamerica (Johnson et al. 2015a,b; Mata-Silva et al.

2015; Terán-Juárez et al. 2016; Woolrich-Piña et al. 2016, 2017; Nevárez-de los Reyes et al. 2016; Cruz-Sáenz et al. 2017; Gonzalez-Sánchez et al. 2017; Lazcano et al. 2019; Ramírez-Bautista et al. 2020; Torres-Hernández et al. 2021; Cruz-Elizalde et al. 2022; Barragán-Vázquez et al. 2022). Johnson (2015a) can be consulted for a statement of this position, with special reference to the subspecies concept.

System for Determining Distributional Status

The system developed by Alvarado-Díaz et al. (2013) for the herpetofauna of Michoacán was applied here to ascertain the distributional status of members of the herpetofauna of Guanajuato. Subsequently, Mata-Silva et al. (2015), Johnson et al. (2015a), Terán-Juárez et al. (2016), Woolrich-Piña et al. (2016, 2017), Nevárez-de los Reyes et al. (2016), Cruz-Sáenz et al. (2017), González-Sánchez et al. (2017), Lazcano et al. (2019), Ramírez-Bautista et al. (2020), Torres-Hernández et al. (2021), Cruz-Elizalde et al. (2022), and Barragán-Vázquez et al. (2022) utilized this system, which consists of three categories in the present paper: CE = endemic to Mexico; NE = not endemic to Mexico; and NN = non-native in Mexico.

Systems for Determining Conservation Status

To assess the conservation status of the herpetofauna of Guanajuato, this study employed the three systems (i.e., SEMARNAT, IUCN, and EVS) used by Alvarado-Díaz et al. (2013), Mata-Silva et al. (2015), Johnson et al. (2015a), Terán-Juárez et al. (2016), Woolrich-Piña et al. (2016, 2017), Nevárez-de los Reyes et al. (2016), Cruz-Sánchez et al. (2017), González-Sánchez et al. (2017), Lazcano et al. (2019), Ramírez-Bautista et al. (2020), Torres-Hernández et al. (2021), Cruz-Elizalde et al. (2022), and Barragán-Vázquez et al. (2022). Detailed descriptions of these three systems appear in the earlier papers in this series, and are not repeated here.

The Mexican Conservation Series

The Mexican Conservation Series (MCS) was initiated in 2013, with a study on the herpetofauna of Michoacán (Alvarado-Díaz et al. 2013), as part of a set of five papers designated as the "Special Mexico Issue" of *Amphibian & Reptile Conservation*. The basic format of the entries in the MCS was established in this paper, i.e., an examination of the composition, physiographic distribution, and conservation status of the herpetofauna of a given Mexican state or group of states. Two years later, the MCS was resumed with a paper on the herpetofauna of Oaxaca (Mata-Silva et al. 2015), and that year Johnson et al. (2015a) presented a paper on the herpetofauna of Chiapas. In the ensuing year, three entries in the MCS were published, on Tamaulipas (Terán-Juárez et al. 2016), Nayarit (Woolrich-Piña et al. 2016), and Nuevo León (Nevárez-de los Reyes et al. 2016). Three more entries were published the following year, on Jalisco (Cruz-Sáenz et al. 2017), the Mexican Yucatan Peninsula (González-Sánchez et al. 2017), and Puebla (Woolrich-Piña et al. 2017). These entries were followed by an article on Coahuila (Lazcano et al. 2019) and another on Hidalgo (Ramírez-Bautista et al. 2020). In the most recent two years, papers on Veracruz (Torres-Hernández et al. 2021), Querétaro (Cruz-Elizalde et al. 2022), and Tabasco (Barragán-Vázquez et al. 2022) were published. Thus, this paper on the herpetofauna of Guanajuato is the 15th entry in the MCS series.

Physiography and Climate

Physiographic Regions

The state of Guanajuato contains a diversity of landscapes, flora, and fauna, which is found within the three physiographic regions recognized here: the Sierra Madre Oriental, the Central Plateau, and the Transmexican Volcanic Belt.

Sierra Madre Oriental (SMO). The Sierra Madre Oriental is a mountain chain located in the eastern portion of Mexico, outlining the Gulf coastal region, from Chihuahua (Parras), Coahuila, San Luis Potosí, Nuevo León, Hidalgo, Veracruz, Puebla, Tlaxcala, Querétaro, and Guanajuato, to the Zongolica region in Veracruz, at elevations above 1,500 m (Morrone 2001; Chávez-Cabello et al. 2011). The SMO is characterized by the presence of a set of minor mountain ranges with folded sedimentary and marine strata (e.g., limestone, shale, and sandstone), which were formed during the Cretaceous-Jurassic periods (Oliva-Aguilar 2012). The SMO is associated with the Gulf of Mexico and it is connected with the TMB and the CP, so is considered a province of Neotropical origin given its temperate and semi-warm climates that support most of the montane cloud forests in the country, primarily in the states of Hidalgo, Puebla, and Veracruz (Morrone 2001; Rzedowski 2006; Cruz-Elizalde et al. 2022). In northeastern Guanajuato, the SMO spans elevations ranging from 1,300 to 2,600 m, within the municipalities of San Luis de La Paz, Victoria, Xichú, and Atarjea, which are embedded in the Sierra Gorda and border the states of San Luis Potosí and Querétaro (Oliva-Aguilar 2012). The SMO is characterized by a temperate climate in the southern portion of the Sierra Gorda, which supports pine and oak forests. To the north, in the municipalities of San Luis de La Paz, Xichú, and Victoria, this region is characterized by a semi-warm tropical climate and contains low tropical forest such as in Xichú, which is influenced by the Gulf of Mexico physiographic region, an area that contains the Río Santa María as one of the main tributaries (Rzedowski 2006; INEGI 2009; Cruz-José et al. 2012; Oliva-Aguilar 2012).

No. 1. *Anaxyrus compactilis* (Wiegmann, 1833). The distribution of the Plateau Toad is widely separated into three populations: (1) the northern Sierra Madre of western Chihuahua; (2) the eastern and western slopes of the Sierra Madre in southern Durango and adjacent western Zacatecas; and (3) south-central Zacatecas and the plateau of Jalisco and Aguascalientes eastward to Tlaxcala and Puebla (Frost 2022). This individual came from El Garbanzo, in the municipality of Irapuato. Wilson et al. (2013b) ascertained its EVS as 14, placing it at the lower limit of the high vulnerability category. IUCN has judged its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 2. *Anaxyrus punctatus* (Baird and Girard, 1852). The distribution of the Red-spotted Toad extends from "southeastern California through southern Nevada and southern Utah to southwestern and southeastern Colorado (excluding high elevations) and southwestern Kansas (USA), thence south to southern Baja California, Sinaloa, Aguascalientes, Jalisco, Guanajuato, San Luis Potosí, Hidalgo, and Tamaulipas (Mexico)" (Frost 2022). This individual came from El Garbanzo, in the municipality of Irapuato. Wilson et al. (2013b) calculated its EVS as 5, placing it in the lower portion of the low vulnerability category. IUCN has considered its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by María del Carmen Mendoza-Portilla.*

No. 3. *Incilius occidentalis* (Camerano, 1879). The Pine Toad is a Mexican endemic species distributed from "the mountains of northern Durango southward over much of the Mexican Plateau and the Transvolcanic Belt" (Lemos-Espinal and Dixon 2013: 39). This individual was encountered at El Copal, in the municipality of Irapuato. Wilson et al. (2013b) calculated its EVS as 11, placing it in the lower portion of the medium vulnerability category. IUCN has considered its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 4. *Craugastor augusti* (Dugès, 1879). The distribution of the Common Barking Frog extends from "Arizona to Texas in the United States, and in Mexico from Sonora to Oaxaca, and from Chihuahua, Coahuila, Nuevo León, and Tamaulipas to Puebla" (Lemos-Espinal and Dixon 2013: 42). This juvenile was found at Urirero, in the municipality of Salvatierra. Wilson et al. (2013b) calculated its EVS as 8, placing it in the upper portion of the low vulnerability category. IUCN has evaluated its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

Central Plateau (CP). The Central Plateau is located in the north-central portion of Mexico, in a region known as the Mexican Altiplano (= high plateau), which is characterized by its semi-desert environment with a Nearctic influence (Morrone 2001; Nieto-Samaniego et al. 2005). The CP includes portions of the states of Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Jalisco, Mich-oacán, Puebla, Querétaro, San Luis Potosí, Tlaxcala, and Zacatecas (Cruz-Elizalde et al. 2022). The elevation in this region ranges from 1,700 to 4,000 m. To the south, it is delimited by the Río Balsas depression, to the east by the Sierra Madre Oriental, to the west by the Sierra Madre Occidental, and to the north this region is influenced by the arid areas of the Chihuahuan Desert. Its largest hydrological basin is the Lerma-Santiago system (CONABIO 2008; Domínguez-Domínguez and Pérez-Ponce de León 2009). This region comprises most of northern Guanajuato, and is characterized by underground aquifers and elevations above 2,000 m (e.g., the Sierra de Guanajuato). In addition, the CP is composed of wide plains interrupted by isolated volcanic mountains and small mountain ranges (INEGI 2009; Cruz-José et al. 2012), such as the Sierra Gorda with its intricate topography of volcanic origin (Olivar-Aguilar 2012). The municipalities located in the CP are the northern portions of León, Guanajuato, Juventino Rosas, Celaya, and Apaseo El Grande; the southern portions of Xichú, Victoria, and San Luis de la Paz; as well as Comonfort, Dolores Hidalgo, Doctor, Mora San Miguel de Allende, San José Iturbide, Santa Catarina, and Tierra Blanca (INEGI 2009). Geologically, this region contains the oldest rocks in the state, which are metamorphic rocks from the Triassic-Jurassic period. Importantly, the plains and valleys seen in this physiographic region today were formed during the Quaternary (INEGI 2009). To the south, the CP is delimited to by the Transmexican Volcanic Belt, and to the east by the Sierra Madre Oriental (INEGI 2009; Oliva-Aguilar 2012).

Transmexican Volcanic Belt (TMB). The Transmexican Volcanic Belt is an arc of volcanic mountain ranges (Pico de Orizaba is the highest peak, at 5,636 m asl) that extend across central-southern Mexico from Nayarit (Bahía de San Blas) and Jalisco (Bahía Banderas) eastward in the direction of Veracruz to reach the coast of the Gulf of Mexico; and this belt extends for about 1,000 km from west to east, and from 80 to 230 km from north to south (Gómez-Tuena et al. 2005; Ferrusquía-Villafranca 2007). Based on its geology and tectonics, the TMB is divided into three regions: the western portion includes the coastal area from the Gulf of California to Nayarit and Jalisco; the central portion contains the Taxco-San Miguel de Allende fault system; and the eastern portion extends in the direction of the Gulf of Mexico and has elevations ranging from 1,300 to 3,000 m (Gómez-Tuena et al. 2005).

The TMB covers approximately 45% of the state of Guanajuato (portions in the central and southern parts of the state), and is characterized by the presence of volcanic mountains, calderas, and plains formed by deposits, with El Bajío consisting of a mosaic of landscapes that include alluvial plains, steep mountain ranges, plains, hills, and lakes, including one of the highest elevations of 3,110 m asl at Cerro de Los Agustinos (Oliva-Aguilar 2012; CONABIO 2008). The TMB crosses the southern part of the state from the borders with Jalisco, Michoacán, and Querétaro; the dominant climate in this physiographic region is semi-arid, with temperatures ranging from 15 to 20 °C (INEGI 2009). One of the main tributaries is the Río Lerma, which crosses this region from south to west, in addition to other bodies of water, such as Laguna de Yuriria (Walter and Brooks 2009). The municipalities in the TMB are Huanimaro, Pénjamo, Cuerámaro, Abasolo, Pueblo Nuevo, Irapuato, Villagrán, Romita, Silao, Coroneo, Acámbaro, Jerécuaro, Tarandacuao, Santiago Maravatio, Salvatierra, Tarimoro, Apaseo El Alto, Jaral del Progreso, Valle de Santiago, and those that border the CP to the south including Apaseo El Grande, León, Celaya, Juventino Rosas, and Salamanca.

Climate

Temperature. Table 1 shows the monthly minimum, mean, and maximum temperatures for each of the three recognized physiographic regions in Guanajuato based on the data for numerous localities in each region (37 in the Central Plateau, 68 in the Transmexican Volcanic

Table 1. Monthly minimum, mean ± SD (in parentheses), maximum, and annual temperature data (in °C) for the three physiographic regions of Guanajuato, Mexico. Data were taken from the Network of Climatological Stations (CONAGUA 2021).

Physiographic region	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Central Plateau (n = 37)	10.1 (12.5 ± 1.2) 15.7	11.8 (13.9 ± 1.2) 17.1	13.9 (16.3 ± 1.2) 19.4	16.3 (18.6 ± 1.2) 21.5	17.1 (20.0 ± 1.2) 22.6	16.6 (19.5 ± 1.2) 22.0	16.1 (18.4 ± 1.2) 20.8	16.5 (18.3 ± 1.2) 20.8	15.6 (17.7 ± 1.2) 20.2	13.8 (16.2 ± 1.2) 18.8	12.5 (14.5 ± 1.1) 17.2	11.3 (13.0 ± 1.1) 16.1	16.6
Transmexican Volcanic Belt (n = 68)	5.9 (14.5 ± 1.5) 17.1	6.5 (15.9 ± 1.6) 18.2	8.3 (18.1 ± 1.6) 20.7	11.2 (20.4 ± 1.5) 23.0	13.8 (22.0 ± 1.5) 24.5	14.9 (21.6 ± 1.4) 23.6	14 (20.3 ± 1.3) 22.2	13.7 (19.6 ± 1.3) 21.6	13.4 (19.6 ± 1.3) 21.6	11.2 (18.3 ± 1.4) 20.3	8.4 (16.5 ± 1.4) 18.8	6.2 (15.0 ± 1.5) 17.8	18.5
Sierra Madre Oriental (n = 3)	15.9 (16.7 ± 0.9) 17.7	17.3 (18.4 ± 1.2) 19.7	20.8 (21.7 ± 1.2) 23.1	23.2 (24.1 ± 1.3) 25.8	24.7 (25.7 ± 1.3) 27.1	24.1 (25.0 ± 1.2) 26.3	22.9 (23.8 ± 1.3) 25.2	22.7 (23.7 ± 1.5) 25.4	21.4 (22.5 ± 1.5) 24.2	19.4 (20.7 ± 1.5) 22.3	17.6 (18.9 ± 1.1) 19.8	15.6 (17.0 ± 1.5) 18.6	21.5

No. 5. *Craugastor occidentalis* (Taylor, 1941). The distribution of Taylor's Barking Frog is from "western Michoacán, Colima, and northeastern Jalisco west and north to southern Zacatecas and southern Sinaloa, Mexico" (Frost 2022). This individual was found at Área Natural Protegida Las Musas, in the municipality of Manuel Doblado. Wilson et al. (2013b) determined its EVS as 13, placing it at the upper limit of the medium vulnerability category. IUCN has assessed its conservation status as Data Deficient, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 6. *Dryophytes arenicolor* (Cope, 1866). The distribution of the Canyon Treefrog is in the mountainous and plateau areas of the USA (southern Utah and southern Colorado southward through eastern Arizona, western and northern New Mexico eastward to about Las Vegas, and the Trans-Pecos region of Texas), southward in Mexico to Michoacán, Colima, México, Guerrero, Hidalgo, and Oaxaca (Frost 2022). This individual was photographed in El Ocotero, in the municipality of Xichú. Wilson et al. (2013b) calculated its EVS as 7, placing it in the middle portion of the low vulnerability category. IUCN has evaluated its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 7. *Hypopachus variolosus* (Cope, 1866). The distribution of the Mexican Narrow-mouthed Toad is in southern Texas (USA), southern Sonora and adjacent southwestern Chihuahua (Mexico) southward in the lowlands and foothills (including the Balsas Depression of southern Mexico) to northern Costa Rica, at elevations mostly below 1,600 m, as well as on Isla Maria Madre in the Tres Marias Archipelago of Nayarit, Mexico (Frost 2022). This individual came from El Potrero within Área Natural Protegida Las Musas, in the municipality of Manuel Doblado. Wilson et al. (2013b) estimated its EVS as 4, placing it in the lower portion of the low vulnerability category. IUCN has judged its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 8. *Lithobates berlandieri* (Baird, 1859). The distribution of the Rio Grande Leopard Frog ranges from "central and western Texas and southern New Mexico (USA) through eastern Chihuahua to central Veracruz and Hidalgo, Mexico; introduced into the lower Colorado River and lower Gila River drainages of Sonora and Baja California del Norte, Mexico, and California and Arizona, USA" (Frost 2022). This individual was found in Xichú, in the municipality of the same name. Wilson et al. (2013b) calculated its EVS as 7, placing it in the middle portion of the low vulnerability category. IUCN has considered its conservation status as Least Concern, and SEMARNAT as a species of Special Protection (Pr). *Photo by Adrian Leyte-Manrique.*

Table 2. Monthly and annual precipitation data (in mm) for the physiographic regions of Guanajuato, Mexico. Data were taken from the Network of Climatological Stations (CONAGUA 2021). The shaded area indicates the months of the rainy season. The monthly values are given as minimum, mean ± SD (in parentheses), and maximum.

Physiographic region	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Central Plateau (n = 37)	4.6 (14.5 ± 6.3) 42.2	2.3 (10.8 ± 3.8) 17.6	0.9 (7.1 ± 2.6) 11.5	7 (14.8 ± 4.4) 27	23.6 (37.7 ± 8.9) 55.7	37.5 (87.5 ± 26.3) 158.8	51.6 (112.5 ± 38.3) 213.2	44.9 (95.5 ± 28.9) 154.5	29.7 (80.7 ± 21.8) 127.8	11.7 (36.4 ± 10.6) 71.1	3.5 (10.3 ± 3.9) 21.2	3.7 (7.5 ± 3.3) 19.1	515.3
Transmexican Volcanic Belt (n = 68)	4 (14.2 ± 4.5) 41.3	1 (9.5 ± 3.1) 17.4	0.6 (5.7 ± 2.2) 12.9	3.6 (9.7 ± 4.3) 25.7	12.8 (29.8 ± 7.0) 46.3	61.1 (111.9 ± 13.8) 138.6	99.7 (158.2 ± 21.9) 209.2	82.2 (138.7 ± 23.0) 222.2	54.7 (107.2 ± 17.4) 159.1	17.8 (42.0 ± 9.1) 68.9	3.5 (9.9 ± 3.4) 21.5	2.2 (6.5 ± 2.2) 13.2	642.9
Sierra Madre Oriental (n = 3)	13.2 (15.2 ± 2.0) 17.2	10.7 (11.0 ± 0.4) 11.4	6.1 (7.8 ± 1.8) 9.7	23.3 (27.4 ± 3.9) 31	29.5 (39.7 ± 10.3) 50.0	74.8 (94.0 ± 17.1) 107.8	86 (115.0 ± 35.9) 155.2	92.6 (102.5 ± 10.4) 113.3	102.4 (121.6 ± 20.1) 142.5	35.2 (54.6 ± 20.8) 76.5	11.4 (15.3 ± 3.4) 17.5	7.7 (9.2 ± 2.3) 11.9	613.4

Belt, and three in the Sierra Madre Oriental). The mean annual temperature is highest in the Sierra Madre Oriental at 21.5 °C, followed by the Transmexican Volcanic Belt at 18.5 °C, and is lowest in the Central Plateau at 16.6 °C.

In the Central Plateau the minimum monthly temperatures range from 10.1 °C in January to 17.1 °C in May, and the monthly maximum temperatures vary from 15.7 °C in January to 22.0 °C in June. In the Transmexican Volcanic Belt, the minimum monthly temperatures range from 5.9 °C in January to 14.9 °C in June, and the monthly maximum temperatures from 17.1 °C in January to 24.5 °C in May. In the Sierra Madre Oriental, the minimum monthly temperatures range from 15.6 °C in December to 24.7 °C in May, and the monthly maximum temperatures from 17.7 °C in January to 27.1 °C in May.

The mean monthly temperatures in the Central Plateau range from 12.5 °C in January to 20.0 °C in May; in the Transmexican Volcan Belt these temperatures range from 14.5 °C in January to 22.0 °C in May; and in the Sierra Madre Oriental they vary from 16.7 °C in January to 25.7 °C in May.

Precipitation. The precipitation regime typically seen in tropical climates also occurs in Guanajuato. In general, this regime is divided into a six-month wet season that extends from May to October, and a dry season from November to April (Table 2).

The mean monthly precipitation is highest in July in the Central Plateau (51.6 mm) and the Transmexican Volcanic Belt (99.7 mm), and in September in the Sierra Madre Oriental (102.4 mm). Based on the mean monthly figures during the rainy season, the percentages of the annual precipitation are 76.4% in the Central Plateau, 86.0% in the Sierra Madre Oriental, and 91.4% in the Transmexican Volcanic Belt. The annual rainfall is lowest in the Central Plateau at 515.3 mm, followed by the Sierra Madre Oriental at 613.4 mm, and highest is in the Transmexican Volcanic Belt at 642.9 mm.

Composition of the Herpetofauna

Families

The species of amphibians and reptiles in Guanajuato are arranged in 25 families, including seven families of anurans, two of salamanders, 14 of squamates, and two of turtles (Table 3). No families of caecilians or crocodylians are represented in the state. The total of 25 families comprises 45.5% of the 55 families represented in Mexico (Ramírez-Bautista et al., In Press). Among the nine families of amphibians, 56.7% (17) of the 30 species (Table 4) are in the families Bufonidae (five), Hylidae (six), and Ranidae (six). Among the 16 families of reptiles, 71.6% (53) of the 74 species (Table 4) are in the families Phrynosomatidae (10), Colubridae (18), Dipsadidae (11), Natricidae (nine), and Viperidae (five).

Genera

Fifty-four herpetofaunal genera are represented in Guanajuato, including 11 genera of anurans, three of salamanders, 38 of squamates, and two of turtles (Table 3). These 54 genera constitute 25.0% of the 216 known from Mexico (Ramírez-Bautista et al., in press). Among the amphibians (Table 4), the most speciose genera are *Eleutherodactylus* (three), *Dryophytes* (three), and *Lithobates* (six). Among the reptiles (Table 4), the most speciose genera are *Sceloporus* (eight), *Plestiodon* (three), *Masticophis* (three), *Geophis* (four), *Rhadinaea* (three), *Thamnophis* (six), and *Crotalus* (five).

Species

The herpetofauna of Guanajuato consists of 101 species, including 24 anurans, three salamanders, 71 squamates, and three turtles (Table 3). Of these 101 species, 96 are native to the state and five are non-native. Currently, the numbers of native species in these groups are 255, 161, 920, and 53, respectively (Ramírez-Bautista et al.,

Table 3. Composition of the native and non-native herpetofauna of Guanajuato, Mexico.

Order	Families	Genera	Species
Anura	7	11	24
Caudata	2	3	3
Subtotal	**9**	**14**	**27**
Squamata	14	38	71
Testudines	2	2	3
Subtotal	**16**	**40**	**74**
Total	**25**	**54**	**101**

Fig. 1. Physiographic regions in the state of Guanajuato, Mexico.

In Press). The 96 native species in Guanajuato constitute 6.9% of the 1,395 native species in all of Mexico (Ramírez-Bautista et al., In Press).

Patterns of Physiographic Distribution

We recognize three physiographic regions in Guanajuato (Fig. 1), and the distribution of members of the herpetofauna among these three regions is documented in Table 4 and summarized in Table 5.

The numbers of species in the three physiographic regions range from a low of 60 in the Central Plateau (CP) to a high of 75 in the Sierra Madre Oriental (SMO). The percentages of the entire state herpetofauna in each of the three physiographic regions, in order of size, are (60/101) 59.4% (CP), (74/101) 73.3% (TVB), and (75/101) 74.3% (SMO). The mean percentage of occupancy is 69.0%.

Among the amphibians and reptiles represented in Guanajuato, the numbers of species are similar for the two larger groups found in the Transmexican Volcanic Belt (TVB) and the Sierra Madre Oriental (SMO), with 74 and 75 species, respectively. The numbers of species in the four orders in these two regions are, respectively, anurans (19 and 18), salamanders (two and three), squamates (50 and 51), and turtles (three and three).

The members of the Guanajuato herpetofauna occupy from one to three of the three physiographic regions, as follows: one (33; 32.7%); two (28; 27.7%); and three (40; 39.6%). The average regional occupancy is 2.1, indicating that each species inhabits about two-thirds of the physiographic regions in the state.

A sizable portion of the herpetofauna occupies either one or two regions (61 or 60.4% of the total of 101 species). As in most of the previous MCS studies, this situation is of considerable conservation significance, and we discuss it in detail in the section on conservation status below.

The numbers of species inhabiting a single region range from none in the Central Plateau (CP) to 22 in the Sierra Madre Oriental (SMO). The intermediate number of 10 is found in the Transmexican Volcanic Belt (TVB). The 22 single-region species in the SMO are:

Incilius nebulifer
Rhinella horribilis
*Rheohyla miotympanum**
*Aquiloeurycea cephalica**
*Abronia taeniata**

Table 4. Distribution of the amphibians, squamates, and turtles of Guanajuato, Mexico, by physiographic region. Abbreviations are as follows: CP = Central Plateau, TVB = Transmexican Volcanic Belt, and SMO = Sierra Madre Oriental. See text for descriptions of these regions. * = species endemic to Mexico and ** = non-native species.

	Physiographic region			Number of regions occupied
Taxa	**CP**	**TVB**	**SMO**	
Anura (24 species)				
Bufonidae (5 species)				
*Anaxyrus compactilis**	+	+		2
Anaxyrus punctatus	+	+	+	3
Incilius nebulifer			+	1
*Incilius occidentalis**	+	+	+	3
Rhinella horribilis			+	1
Craugastoridae (2 species)				
Craugastor augusti	+	+	+	3
*Craugastor occidentalis**		+		1
Eleutherodactylidae (3 species)				
*Eleutherodactylus angustidigitorum**		+	+	2
Eleutherodactylus guttilatus	+	+	+	3
*Eleutherodactylus verrucipes**	+		+	2
Hylidae (6 species)				
Dryophytes arenicolor	+	+	+	3
*Dryophytes eximius**	+	+	+	3
*Dryophytes plicata**		+	+	2
*Rheohyla miotympanum**			+	1
Smilisca baudinii	+		+	2
Smilisca fodiens		+		1
Microhylidae (1 species)				
Hypopachus variolosus	+	+	+	3
Ranidae (6 species)				
Lithobates berlandieri	+	+	+	3
*Lithobates catesbeianus***		+		1
*Lithobates megapoda**	+	+		2
*Lithobates montezumae**	+	+	+	3
*Lithobates neovolcanicus**	+	+		2
*Lithobates spectabilis**	+	+	+	3
Scaphiopodidae (1 species)				
Spea multiplicata	+	+	+	3
Caudata (3 species)				
Ambystomatidae (1 species)				
*Ambystoma velasci**	+	+	+	3
Plethodontidae (2 species)				
*Aquiloeurycea cephalica**			+	1
*Isthmura bellii**	+	+	+	3
Squamata (71 species)				
Anguidae (4 species)				
*Abronia taeniata**			+	1
*Barisia imbricata**	+	+	+	3
Gerrhonotus infernalis	+	+	+	3
Gerrhonotus liocephalus		+		1
Dactyloidae (2 species)				
*Norops nebulosus**	+	+		2
Norops sericeus			+	1
Gekkonidae (2 species)				
*Hemidactylus frenatus***		+		1
*Hemidactylus turcicus***		+		1
Phrynosomatidae (10 species)				
Holbrookia maculata			+	1

Table 4 (continued). Distribution of the amphibians, squamates, and turtles of Guanajuato, Mexico, by physiographic region. Abbreviations are as follows: CP = Central Plateau, TVB = Transmexican Volcanic Belt, and SMO = Sierra Madre Oriental. See text for descriptions of these regions. * = species endemic to Mexico and ** = non-native species.

	Physiographic region			Number of regions occupied
Taxa	**CP**	**TVB**	**SMO**	
*Phrynosoma orbiculare**	+	+	+	3
*Sceloporus aeneus**	+	+		2
*Sceloporus dugesii**	+	+		2
Sceloporus grammicus	+	+	+	3
*Sceloporus minor**	+		+	2
*Sceloporus scalaris**	+	+	+	3
*Sceloporus spinosus**	+	+	+	3
*Sceloporus torquatus**	+	+	+	3
Sceloporus variabilis			+	1
Scincidae (3 species)				
*Plestiodon dugesii**		+		1
*Plestiodon lynxe**		+	+	2
Plestiodon tetragrammus			+	1
Sphenomorphidae (1 species)				
*Scincella silvicola**			+	1
Teiidae (1 species)				
Aspidoscelis gularis	+	+	+	3
Xantusiidae (2 species)				
*Lepidophyma gaigeae**			+	1
*Lepidophyma occulor**			+	1
Boidae (1 species)				
Boa imperator			+	1
Colubridae (18 species)				
*Conopsis lineata**	+	+	+	3
*Conopsis nasus**	+	+	+	3
Drymarchon melanurus	+	+	+	3
*Lampropeltis mexicana**		+	+	2
*Lampropeltis polyzona**	+	+		2
*Leptophis diplotropis**	+	+		2
Masticophis flagellum		+	+	2
Masticophis mentovarius	+	+	+	3
Masticophis schotti			+	1
Oxybelis microphthalmus		+	+	2
Pantherophis emoryi			+	1
*Pituophis deppei**	+	+	+	3
*Pseudoficimia frontalis**	+	+		2
*Salvadora bairdi**	+	+	+	3
Senticolis triaspis	+	+	+	3
*Tantilla bocourti**	+	+	+	3
Tantilla rubra			+	1
Trimorphodon tau	+	+	+	3
Dipsadidae (11 species)				
Diadophis punctatus	+	+		2
*Geophis dugesii**		+		1
*Geophis latifrontalis**			+	1
*Geophis petersii**		+		1
Geophis sartorii			+	1
Hypsiglena jani	+	+	+	3
*Hypsiglena tanzeri**	+	+	+	3
Leptodeira septentrionalis			+	1
*Rhadinaea gaigeae**			+	1
*Rhadinaea hesperia**	+	+		2

Table 4 (continued). Distribution of the amphibians, squamates, and turtles of Guanajuato, Mexico, by physiographic region. Abbreviations are as follows: CP = Central Plateau, TVB = Transmexican Volcanic Belt, and SMO = Sierra Madre Oriental. See text for descriptions of these regions. * = species endemic to Mexico and ** = non-native species.

	Physiographic region			Number of regions occupied
Taxa	CP	TVB	SMO	
*Rhadinaea taeniata**			+	1
Elapidae (1 species)				
Micrurus tener	+	+	+	3
Natricidae (9 species)				
*Adelophis copei**		+		1
Storeria dekayi			+	1
*Storeria storerioides**	+	+	+	3
Thamnophis cyrtopsis	+	+	+	3
Thamnophis eques	+	+		2
*Thamnophis melanogaster**	+	+		2
*Thamnophis pulchrilatus**		+	+	2
*Thamnophis scalaris**	+	+	+	3
*Thamnophis scaliger**	+	+		2
Typhlopidae (1 species)				
*Virgotyphlops braminus***	+	+		2
Viperidae (5 species)				
*Crotalus aquilus**	+	+	+	3
Crotalus atrox			+	1
Crotalus molossus	+	+	+	3
*Crotalus polystictus**	+	+		2
Crotalus scutulatus	+		+	2
Testudines (3 species)				
Emydidae (1 species)				
*Trachemys scripta***		+	+	2
Kinosternidae (2 species)				
Kinosternon hirtipes	+	+	+	3
*Kinosternon integrum**	+	+	+	3
Total (101 species)	**60**	**74**	**75**	—

Norops sericeus
Holbrookia maculata
Sceloporus variabilis
Plestiodon tetragrammus
*Scincella silvicola**
*Lepidophyma gaigeae**
*Lepidophyma occulor**
Boa imperator
Masticophis schotti
Pantherophis emoryi
Tantilla rubra
*Geophis latifrontalis**
Leptodeira septentrionalis
*Rhadinaea gaigeae**
*Rhadinaea taeniata**
Storeria dekayi
Crotalus atrox

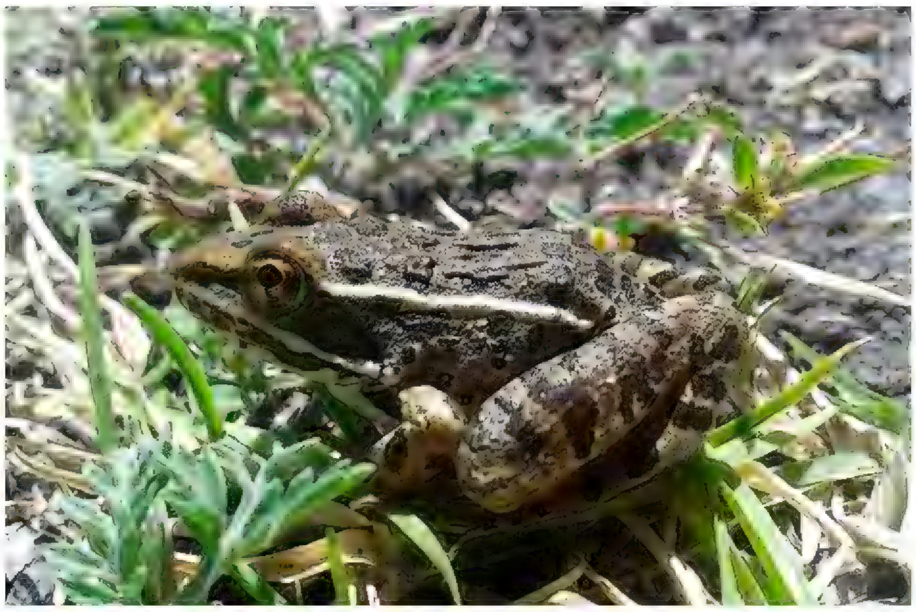
As the single asterisks indicate country endemics, 13 of the 22 SMO single-region species are non-endemics (59.1%) and nine are country endemics (40.9%).

The 10 single-region species in the TVB are:

*Craugastor occidentalis**
Smilisca fodiens
*Lithobates catesbeianus***
Gerrhonotus liocephalus
*Hemidactylus frenatus***
*Hemidactylus turcicus***
*Plestiodon dugesii**
*Geophis dugesii**
*Geophis petersii**
*Adelophis copei**

Five of the 10 single-region TVB species are country endemics (50.0%), two are non-endemics (20.0%), and the three indicated by double-asterisks are non-natives (30.0%).

In summary, of the 32 single-region species, 15 are non-endemics (46.9%), 14 are country endemics (43.8%), and three are non-natives (9.4%). Of the three physiographic regions, the SMO has considerable conservation significance (but see section on Relative Herpetofaunal Priority), inasmuch as it contains the highest numbers of species (75 of 101, or 74.3%), country endemics (37 of 56, or 66.1%), and single-region species (22 of 32, or 68.8%).



No. 9. *Lithobates neovolcanicus* (Hillis and Frost, 1985). The distribution of the Transverse Volcanic Leopard Frog is in pine-oak forest and mesquite-grassland at elevations from 1,500 to 2,500 m along the southern edge of the Mexican Plateau in the states of Guanajuato, Jalisco, Colima, Zacatecas, Michoacán, México, and Hidalgo, Mexico (Frost 2022). This individual came from San Nicolás de los Agustinos, in the municipality of Salvatierra. Wilson et al. (2013b) calculated its EVS as 13, placing it at the upper limit of the medium vulnerability category. IUCN has judged its conservation status as Near Threatened, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 10. *Spea multiplicata* (Cope, 1863). The distribution of the Mexican Spade-foot Toad is in southeastern Utah and southern Colorado through western Oklahoma, Arizona, New Mexico, and West Texas, in the USA, southward to the southern edge of the Mexican Plateau as far as Nayarit, Guerrero, Oaxaca, Hidalgo, and Tlaxcala, Mexico, at elevations from sea level to 2,743 m (Frost 2022). This individual came from La Torrecilla within Área Natural Protegida Las Musas, in the municipality of Manuel Doblado. Wilson et al. (2013b) reported its EVS as 6, placing it in the middle of the low vulnerability category. IUCN has not evaluated its conservation status, and SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 11. *Ambystoma velasci* (Dugés, 1888). The Plateau Tiger Salamander is a Mexican endemic occurring from "northwestern Chihuahua south along the eastern slope of the Sierra Madre Occidental and southern Nuevo Leon to Hidalgo in the Sierra Madre Oriental, west to Zacatecas, and south into the Transverse Volcanic range of central Mexico" (Frost 2022). This individual was photographed in pine-oak forest within the Reserva de la Biósfera Sierra Gorda in the community of El Ocotero, in the municipality of Xichú. Wilson et al. (2013b) calculated its EVS as 10, placing it at the lower limit of the medium vulnerability category. IUCN has considered its conservation status as Least Concern, and SEMARNAT as a species of Special Protection (Pr). *Photo by Adrian Leyte-Manrique.*

No. 12. *Isthmura bellii* (Gray, 1850). Bell's Salamander is a Mexican endemic occurring from "southern Tamaulipas, Tlaxcala, Hidalgo and the Sierra Madre del Sur of Guerrero, Mexico, and west and north to southern Nayarit and southern Zacatecas" (Frost 2022). This individual was found in the Sierra de los Agustinos, in the municipality of Guanajuato. Wilson et al. (2013b) established its EVS as 12, placing it in the upper portion of the medium vulnerability category. IUCN has judged its conservation status as Vulnerable, and SEMARNAT lists this species as Threatened (A). *Photo by José Carlos Arenas-Monroy.*

Table 5. Summary of the distributional occurrence of herpetofaunal families in Guanajuato, Mexico, by physiographic province. See Table 4 for an explanation of the abbreviations.

Family	Number of species	Distributional occurrence		
		CP	TVB	SMO
Bufonidae	5	3	3	4
Craugastoridae	2	1	2	1
Eleutherodactylidae	3	2	2	3
Hylidae	6	3	4	5
Microhylidae	1	1	1	1
Ranidae	6	5	6	3
Scaphiopodidae	1	1	1	1
Subtotal	**24**	**16**	**19**	**18**
Ambystomatidae	1	1	1	1
Plethodontidae	2	1	1	2
Subtotal	**3**	**2**	**2**	**3**
Total	**27**	**18**	**21**	**21**
Anguidae	4	2	3	3
Dactyloidae	2	1	1	1
Gekkonidae	2	—	2	—
Phrynosomatidae	10	8	7	8
Scincidae	3	—	2	2
Sphenomorphidae	1	—	—	1
Teiidae	1	1	1	1
Xantusiidae	2	—	—	2
Subtotal	**25**	**12**	**16**	**18**
Boidae	1	—	—	1
Colubridae	18	12	15	15
Dipsadidae	11	4	6	7
Elapidae	1	1	1	1
Natricidae	9	6	8	5
Typhlopidae	1	1	1	—
Viperidae	5	4	3	4
Subtotal	**46**	**28**	**34**	**33**
Emydidae	1	—	1	1
Kinosternidae	2	2	2	2
Subtotal	**3**	**2**	**3**	**3**
Total	**74**	**42**	**53**	**54**
Sum Total	**101**	**60**	**74**	**75**

A Coefficient of Biogeographic Resemblance (CBR) matrix was constructed using the Duellman (1990) algorithm to assess the herpetofaunal similarity relationships among the three physiographic regions in Guanajuato (Table 6). These data were then used to produce a UPGMA dendrogram (Fig. 10; Sokal and Michener 1958). The SMO harbors the greatest amount of species richness (75 species), and the CP has the least (60 species). The average species richness value for the three regions is 69.7. The lowest number of shared species (44) is between the CP and the SMO, which is interesting inasmuch as these two regions of the state abut one another. The highest number of shared species (56) is between the CP and the TVB, two regions that also contact one another.

Distribution Status Categorizations

The system employed by Alvarado-Díaz et al. (2013) and the remainder of the MCS entries (see above) was used to analyze the distributional status of members of the Guanajuato herpetofauna. The three categories that apply to the Guanajuato herpetofauna are non-endemic, country endemic, and non-native. No state endemic

Table 6. Pair-wise comparison matrix of Coefficient of Biogeographic Resemblance (CBR) data for the herpetofaunal relationships between the three physiographic regions in Guanajuato, Mexico. Underlined values = number of species in each region; upper triangular matrix values = species in common between two regions; and lower triangular matrix values = CBR values. The formula for this algorithm is CBR = $2C/N_1 + N_2$ (Duellman 1990), where C is the number of species in common to both regions, N_1 is the number of species in the first region, and N_2 is the number of species in the second region. See Fig. 10 for the UPGMA dendrogram produced from the CBR data.

	Central Plateau	Transmexican Volcanic Belt	Sierra Madre Oriental
Central Plateau	<u>60</u>	56	44
Transmexican Volcanic Belt	0.84	<u>74</u>	48
Sierra Madre Oriental	0.65	0.73	<u>75</u>

species are known to occur in Guanajuato. The basic data are given in Table 7 and summarized in Table 8.

The numbers of species in each of these three categories, in descending order of size, are as follows: country endemics, 56 (55.4%); non-endemics, 40 (39.6%); and non-natives, five (5.0%). In this fashion, the Guanajuato herpetofauna resembles those of many of the other states dealt with in the MCS, i.e., the largest number of species occupies the country endemic category, as was found in Michoacán (Alvarado-Díaz et al. 2013), Nayarit (Woolrich-Piña et al. 2016), Jalisco (Cruz Sáenz et al. 2017), Puebla (Woolrich-Piña et al. 2017), Hidalgo (Ramírez-Bautista et al. 2020), and Querétaro (Cruz-Elizalde et al. 2022). In other states, the number of non-endemic species exceeds that of the country endemic species: Oaxaca (Mata-Silva et al. 2015); Chiapas (Johnson et al. 2015a); Tamaulipas (Terán-Juárez et al. 2016); Nuevo León (Nevárez-de los Reyes et al. 2016); the Mexican Yucatan Peninsula (González-Sánchez et al. 2017), Coahuila (Lazcano et al. 2019), Veracruz (Torres-Hernández et al. 2021), and Tabasco (Barragán-Vázquez et al. 2022).

As noted above, in some instances in the MCS the number of country endemics is higher than the number of non-endemic species, whereas in other cases the reverse is true. Therefore, the ratios of country endemics to non-endemic species vary extensively. The ratios in which the number of country endemics is higher than the number of non-endemics range from 0.53 in the case of Jalisco to 0.88 in Hidalgo. The ratios in which the number of non-endemics exceeds the number of country endemics range from 1.12 in the case of Oaxaca (Mata-Silva et al. 2015) to 127.0 in the Yucatan Peninsula (González-Sánchez et al. 2017). In general, the nature of this ratio depends on how close the state in question is to either the United States or Central America. This ratio also depends upon the size of these two aspects of a given herpetofauna as to whether the ratio will be more or less than one.

Fig. 2. Water pool in low deciduous forest in the community of La Torrecilla, Manuel Doblado, Las Musas Natural Protected Area, Transmexican Volcanic Belt. *Photo by Ma. del Carmen Mendoza-Portilla.*

Fig. 3. Panoramic view of Cerro de "El Veinte." The vegetation consists of low deciduous forest, with agricultural crops in the background. Town of Cuchicuato, Irapuato, Guanajuato, in the Transmexican Volcanic Belt. *Photo by Adrian Leyte-Manrique.*

Fig. 4. Cerro de Tetillas. Low deciduous forest near Janicho, Salvatierra, south of Guanajuato. This area is an agricultural region in the Transmexican Volcanic Belt. *Photo by Adrian Leyte-Manrique.*

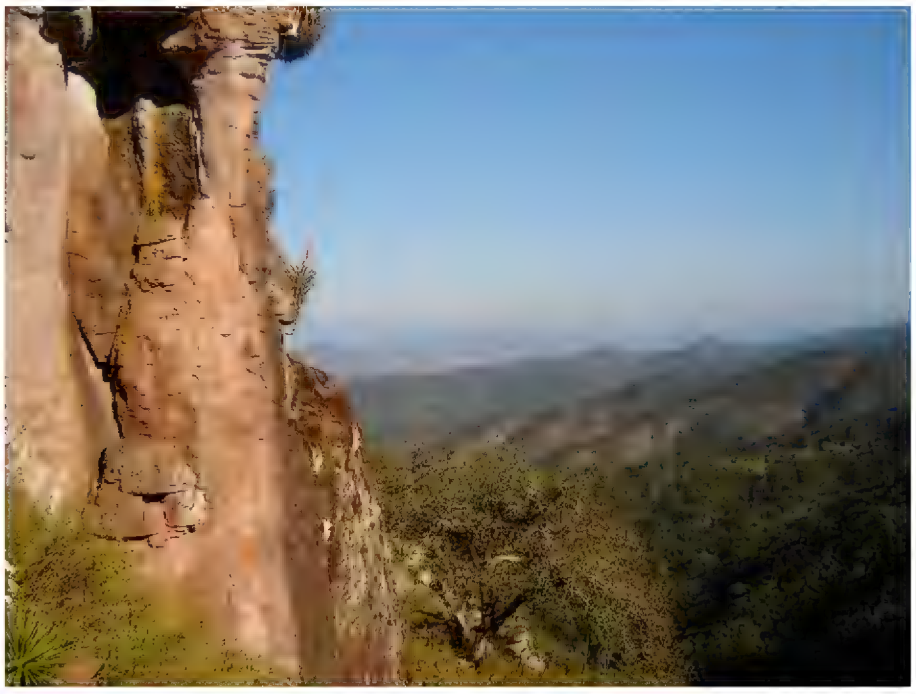


Fig. 5. A mountain range at Vergel de Bernalejo, in the municipality of San Luis de la Paz, Guanajuato in the Sierra Madre Oriental physiographic region. *Photo by Oscar Báez-Montes*.

Table 7. Distributional and conservation status measures for members of the herpetofauna of Guanajuato, Mexico. Distributional status: CE = endemic to country of Mexico; NE = not endemic to state or country; and NN = non-native. The numbers suffixed to the NE category signify the distributional categories developed by Wilson et al. (2017) and implemented in the taxonomic list at the Mesoamerican Herpetology website (http://mesoamericanherpetology.com), as follows: 3 (species distributed only in Mexico and the United States); 6 (species ranging from Mexico to South America); 7 (species ranging from the United States to Central America); and 8 (species ranging from the United States to South America). Environmental Vulnerability Score categories (taken from Wilson et al. 2013a,b): low (L) vulnerability species (EVS of 3–9); medium (M) vulnerability species (EVS of 10–13); and high (H) vulnerability species (EVS of 14–20). IUCN categorization: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient; NE = Not Evaluated. SEMARNAT Status: A = Threatened; P = Endangered; Pr = Special Protection; and NS = No Status. See Alvarado-Díaz et al. (2013), Johnson et al. (2015a), and Mata-Silva et al. (2015) for explanations of the EVS, IUCN, and SEMARNAT rating systems.

Species	Distributional status	Environmental Vulnerability Category (score)	IUCN categorization	SEMARNAT status
*Anaxyrus compactilis**	CE	H (14)	LC	NS
Anaxyrus punctatus	NE3	L (5)	LC	NS
Incilius nebulifer	NE3	L (6)	LC	NS
*Incilius occidentalis**	CE	M (11)	LC	NS
Rhinella horribilis	NE7	L (3)	NE	NS
Craugastor augusti	NE3	L (8)	LC	NS
*Craugastor occidentalis**	CE	M (13)	DD	NS
*Eleutherodactylus angustidigitorum**	CE	H (17)	VU	Pr
Eleutherodactylus guttilatus	NE3	M (11)	LC	NS
*Eleutherodactylus verrucipes**	CE	H (16)	VU	Pr
Dryophytes arenicolor	NE3	L (7)	LC	NS
*Dryophytes eximius**	CE	M (10)	LC	NS
*Dryophytes plicata**	CE	M (11)	LC	A
*Rheohyla miotympanum**	CE	L (9)	NT	NS
Smilisca baudinii	NE7	L (3)	LC	NS
Smilisca fodiens	NE3	L (8)	LC	NS
Hypopachus variolosus	NE7	L (4)	LC	NS
Lithobates berlandieri	NE3	L (7)	LC	Pr
Lithobates catesbeianus	NN	—	—	—
*Lithobates megapoda**	CE	H (14)	VU	Pr
*Lithobates montezumae**	CE	M (13)	LC	Pr
*Lithobates neovolcanicus**	CE	M (13)	NT	A
*Lithobates spectabilis**	CE	M (12)	LC	NS
Spea multiplicata	NE3	L (6)	LC	NS
*Ambystoma velasci**	CE	M (10)	LC	Pr
*Aquiloeurycea cephalica**	CE	H (14)	NT	A
*Isthmura bellii**	CE	M (12)	VU	A
*Abronia taeniata**	CE	H (15)	VU	Pr
*Barisia imbricata**	CE	H (14)	LC	Pr
Gerrhonotus infernalis	NE3	M (13)	LC	NS
Gerrhonotus liocephalus	NE3	L (6)	LC	Pr
*Norops nebulosus**	CE	M (13)	LC	NS
Norops sericeus	NE4	L (8)	NE	NS
*Hemidactylus frenatus***	NN	—	—	—
*Hemidactylus turcicus***	NN	—	—	—
Holbrookia maculata	NE3	M (10)	LC	NS
*Phrynosoma orbiculare**	CE	M (12)	LC	A
*Sceloporus aeneus**	CE	M (13)	LC	NS
*Sceloporus dugesii**	CE	M (13)	LC	NS
Sceloporus grammicus	NE3	L (9)	LC	Pr
*Sceloporus minor**	CE	H (14)	LC	NS
*Sceloporus scalaris**	CE	M (12)	LC	NS
*Sceloporus spinosus**	CE	M (12)	LC	NS
*Sceloporus torquatus**	CE	M (11)	LC	NS
Sceloporus variabilis	NE4	L (5)	LC	NS
*Plestiodon dugesii**	CE	H (16)	VU	Pr
*Plestiodon lynxe**	CE	M (10)	LC	Pr
Plestiodon tetragrammus	NE3	M (12)	LC	NS
*Scincella silvicola**	CE	M (12)	LC	A
Aspidoscelis gularis	NE3	L (9)	LC	NS
*Lepidophyma gaigeae**	CE	M (13)	VU	Pr
*Lepidophyma occulor**	CE	H (14)	LC	Pr
Boa imperator	NE6	M (10)	NE	NS

Table 7 (continued). Distributional and conservation status measures for members of the herpetofauna of Guanajuato, Mexico. Distributional status: CE = endemic to country of Mexico; NE = not endemic to state or country; and NN = non-native. The numbers suffixed to the NE category signify the distributional categories developed by Wilson et al. (2017) and implemented in the taxonomic list at the Mesoamerican Herpetology website (http://mesoamericanherpetology.com), as follows: 3 (species distributed only in Mexico and the United States); 6 (species ranging from Mexico to South America); 7 (species ranging from the United States to Central America); and 8 (species ranging from the United States to South America). Environmental Vulnerability Score categories (taken from Wilson et al. 2013a,b): low (L) vulnerability species (EVS of 3–9); medium (M) vulnerability species (EVS of 10–13); and high (H) vulnerability species (EVS of 14–20). IUCN categorization: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient; NE = Not Evaluated. SEMARNAT Status: A = Threatened; P = Endangered; Pr = Special Protection; and NS = No Status. See Alvarado-Díaz et al. (2013), Johnson et al. (2015a), and Mata-Silva et al. (2015) for explanations of the EVS, IUCN, and SEMARNAT rating systems.

Species	Distributional status	Environmental Vulnerability Category (score)	IUCN categorization	SEMARNAT status
*Conopsis lineata**	CE	M (13)	LC	NS
*Conopsis nasus**	CE	M (11)	LC	NS
Drymarchon melanurus	NE6	L (6)	LC	NS
*Lampropeltis mexicana**	CE	H (15)	LC	A
*Lampropeltis polyzona**	CE	M (11)	NE	NS
*Leptophis diplotropis**	CE	H (14)	LC	A
Masticophis flagellum	NE3	L (8)	LC	A
Masticophis mentovarius	NE6	L (6)	LC	A
Masticophis schotti	NE3	M (13)	LC	NS
Oxybelis microphthalmus	NE3	M (11)	NE	NS
Pantherophis emoryi	NE3	M (13)	LC	NS
*Pituophis deppei**	CE	H (14)	LC	A
*Pseudoficimia frontalis**	CE	M (13)	LC	NS
*Salvadora bairdi**	CE	H (15)	LC	Pr
Senticolis triaspis	NE7	L (6)	LC	NS
*Tantilla bocourti**	CE	L (9)	LC	NS
Tantilla rubra	NE4	L (5)	LC	Pr
*Trimorphodon tau**	CE	M (13)	LC	NS
Diadophis punctatus	NE3	L (4)	LC	NS
*Geophis dugesii**	CE	M (13)	LC	NS
*Geophis latifrontalis**	CE	H (14)	DD	Pr
*Geophis petersii**	CE	H (15)	DD	Pr
Geophis sartorii	NE4	L (9)	LC	Pr
Hypsiglena jani	NE3	L (6)	NE	NS
*Hypsiglena tanzeri**	CE	H (15)	DD	NS
Leptodeira septentrionalis	NE8	L (8)	NE	NS
*Rhadinaea gaigeae**	CE	M (12)	DD	NS
*Rhadinaea hesperia**	CE	M (10)	LC	Pr
*Rhadinaea taeniata**	CE	M (13)	LC	NS
Micrurus tener	NE3	M (11)	LC	NS
*Adelophis copei**	CE	H (15)	VU	Pr
Storeria dekayi	NE7	L (7)	LC	NS
*Storeria storerioides**	CE	M (11)	LC	NS
Thamnophis cyrtopsis	NE7	L (7)	LC	A
Thamnophis eques	NE3	L (8)	LC	A
*Thamnophis melanogaster**	CE	H (15)	EN	A
*Thamnophis pulchrilatus**	CE	H (15)	LC	NS
*Thamnophis scalaris**	CE	H (14)	LC	A
*Thamnophis scaliger**	CE	H (15)	VU	A
*Virgotyphlops braminus***	NN	—	—	—
*Crotalus aquilus**	CE	H (16)	LC	Pr
Crotalus atrox	NE3	L (9)	LC	Pr
Crotalus molossus	NE3	L (8)	LC	Pr
*Crotalus polystictus**	CE	H (16)	LC	Pr
Crotalus scutulatus	NE3	M (11)	LC	Pr
Trachemys scripta	NN	—	—	—
Kinosternon hirtipes	NE3	M (10)	LC	Pr
*Kinosternon integrum**	CE	M (11)	LC	Pr

Fig. 6. Small seasonal wetlands used to store water in the Central Plateau at San Jose del Llano, in the municipality of San Felipe, Guanajuato. *Photo by Yadira Fabiola Estrada-Sillas.*

Fig. 7. Xeric scrub along the Central Plateau, in the municipality of San Felipe, Guanajuato. *Photo by Oscar Báez-Montes.*

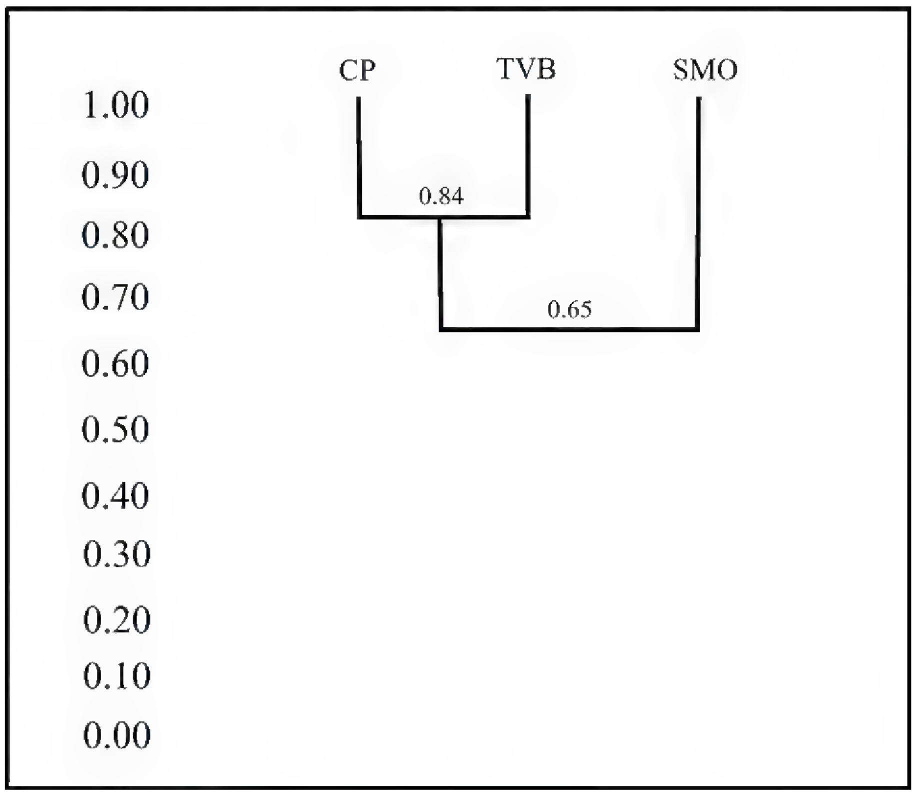
Fig. 8. An agricultural landscape with patches of native vegetation and isolated hills at Chicamito, in the municipality of Valle de Santiago, Guanajuato, Transmexican Volcanic Belt. *Photo by Oscar Báez-Montes.*

Fig. 9. A water pool and pine-oak vegetation at Charco Azul, Xichú, Guanajuato, in the Sierra Gorda-Guanajuato Biosphere Reserve, located in the Sierra Madre Oriental. *Photo by Adrian Leyte-Manrique.*

So, we would expect that the herpetofaunas of states more or less equidistant from both the USA and Central America (Guatemala and/or Belize) would have ratios closer to one. As noted in Torres-Hernández et al. (2021): "In the case of the three MCS states that border the USA, the ratios are 3.22 (100/31 in Coahuila; Lazcano et al. 2019), 2.44 (95/39 in Nuevo León; Navárez-de los Reyes et al. 2016), and 2.32 (130/56 in Tamaulipas; Terán-Juárez et al. 2016). In the case of the states or the region sharing a border with Central America, the ratios are 8.38 (268/32 in Chiapas; Johnson et al. 2015a) and 127.0 (127/1 in the Yucatan Peninsula; González-Sánchez et al. 2017). The extremely high ratio for the Yucatan Peninsula is due, at least in part, to this region lying adjacent to its southern portion lying in northern Guatemala."

The five non-native species reported as occurring in Guanajuato are *Lithobates catesbeianus*, *Hemidactylus frenatus*, *H. turcicus*, *Virgotyphlops braminus*, and *Trachemys scripta*. Two of these species (*H. frenatus* and *V. braminus*) are the most widespread of the non-native species recorded in the previous 14 MCS entries, inasmuch as they have been reported in 14 and 15 states, respectively.

Fig. 10. UPGMA generated dendrogram illustrating the similarity relationships of species richness among the herpetofaunal components in the three physiographic regions of Guanajuato (based on the data in Table 6; Sokal and Michener 1958). Similarity values were calculated using the Coefficient of Biogeographic Resemblance (CBR) of Duellman (1990).



No. 13. *Barisia imbricata* (Wiegmann, 1828). The Imbricate Alligator Lizard is a Mexican endemic inhabiting the mountains of the Transmexican Volcanic Belt and the Sierra Madre Occidental in the states of México, Distrito Federal, Querétaro, Hidalgo, Jalisco, Puebla, Michoacán, Morelos, and Tlaxcala; additional isolated populations have been recorded in Oaxaca and Veracruz (Ramírez-Bautista et al. 2014). This individual was found in Sierra del Tigre, in the municipality of Mazamitla. Wilson et al. (2013a) determined its EVS as 14, placing it at the lower limit of the high vulnerability category. IUCN has judged its conservation status as Least Concern, and SEMARNAT as a species of Special Protection (Pr). *Photo by Adrian Leyte-Manrique.*

No. 14. *Norops nebulosus* (Wiegmann, 1834). The Clouded Anole is a Mexican endemic distributed from "Sinaloa to the Isthmus of Tehuantepec on the Pacific coast, extending to the states of Morelos, Puebla, and Durango" (translation ours; Santiago-Pérez et al. 2012: 136). This individual was encountered at Cuchicuato, in the municipality of Irapuato. Wilson et al. (2013a) determined its EVS as 13, placing it at the upper limit of the medium vulnerability category. IUCN has assessed its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 15. *Sceloporus spinosus* (Wiegmann, 1828). The Eastern Spiny Lizard is a widespread endemic species found over much of central Mexico, at elevations from 1,500 to 2,300 m asl (Florez and Gerez 1994). This individual was photographed in Temascatio, in the municipality of Irapuato. Wilson et al. (2013a) ascertained its EVS as 12, placing it in the upper portion of the medium vulnerability category. IUCN has assessed its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 16. *Plestiodon lynxe* (Wiegmann, 1834). The Oak Forest Skink is a Mexican endemic distributed in southern San Luis Potosí, Guanajuato, Querétaro, Hidalgo, and the mountains of western Veracruz, with isolated populations occurring in southern Durango, southwestern Zacatecas, southeastern Nayarit, and Jalisco (Webb 1968; Ponce-Campos and Romero-Contreras 2006; Canseco-Márquez et al. 2007; Lemos-Espinal and Dixon 2013). This individual was encountered at Puente de Camotlán, in the municipality of La Yesca. Wilson et al. (2013a) determined its EVS as 10, placing it at the lower limit of the medium vulnerability category. IUCN has judged its conservation status as Least Concern, and SEMARNAT as a species of Special Protection (Pr). *Photo by Adrian Leyte-Manrique.*

Table 8. Summary of the distributional status of herpetofaunal families in Guanajuato, Mexico.

Family	Number of species	Distributional status		
		Non-endemic (NE)	Country Endemic (CE)	Non-native (NN)
Bufonidae	5	3	2	—
Craugastoridae	2	1	1	—
Eleutherodactylidae	3	1	2	—
Hylidae	6	3	3	—
Microhylidae	1	1	—	—
Ranidae	6	1	4	1
Scaphiopodidae	1	1	—	—
Subtotal	**24**	**11**	**12**	**1**
Ambystomatidae	1	—	1	—
Plethodontidae	2	—	2	—
Subtotal	**3**	**—**	**3**	**—**
Total	**27**	**11**	**15**	**—**
Anguidae	4	2	2	—
Dactyloidae	2	1	1	—
Gekkonidae	2	—	—	2
Phrynosomatidae	10	3	7	—
Scincidae	3	1	2	—
Sphenomorphidae	1	—	1	—
Teiidae	1	1	—	—
Xantusiidae	2	—	2	—
Subtotals	**25**	**8**	**15**	**2**
Boidae	1	1	—	—
Colubridae	18	8	10	—
Dipsadidae	11	4	7	—
Elapidae	1	1	—	—
Natricidae	9	3	6	—
Typhlopidae	1	—	—	1
Viperidae	5	3	2	—
Subtotals	**46**	**20**	**25**	**1**
Emydidae	1	—	—	1
Kinosternidae	2	1	1	—
Subtotal	**3**	**1**	**1**	**1**
Total	**74**	**29**	**41**	**4**
Sum Total	**101**	**40**	**56**	**5**

Wilson et al. (2017) originated a system for categorizing the distribution of the non-endemic species in the Mexican herpetofauna. The categorizations of the 40 non-endemic species in Guanajuato (Table 9) indicate that the largest number of these 40 species (26, or 65.0%) are MXUS species, i.e., those that occur in both Mexico and the United States. The next highest number (six, or 15.0%) are USCA species, i.e., species that range from the United States through Mexico to some point in Central America. The remaining eight species are MXCA species (four, or 10.0%), MXSA species (three, or 7.5%), or USSA species (one, or 2.5%).

Comparisons to the Herpetofaunas of Adjacent States

As noted above, Guanajuato is a state in central Mexico bordered by San Luis Potosí, Querétaro, Michoacán, Jalisco, and a small portion of Zacatecas. The herpetofaunas of three of these five states (Querétaro, Michoacán, and Jalisco) have been dealt with in the Mexican Conservation Series (see above). The herpetofauna of San Luis Potosí has been studied by Lemos-Espinal and Dixon (2013) and Lemos-Espinal et al. (2018). We have not dealt with the herpetofauna of Zacatecas, as the amount of the border shared between these states is very small compared to the length of the border in either state, and because this state has not been dealt with in either the MCS or the series of Lemos-Espinal et al.

In order to compare the herpetofaunas of the four neighboring states (San Luis Potosí, Querétaro, Michoacán, and Jalisco) to that of Guanajuato, a table was constructed (Table 10) that indicates the numbers of species in the various herpetofaunal groups for the five states, along with the numbers of endemic species, non-endemic species, and non-native species, as well as the respective proportions of endemic species in each state.

The numbers of herpetofaunal species per state range from a low of 101 in Guanajuato to a high of 223 in Jalisco. The numbers of non-endemic species range from a low of 40 in Guanajuato to a high of 105 in San Luis

Table 9. Summary of the distributional categories of the herpetofaunal families in Guanajuato, Mexico, that contain non-endemic species. The categorizations are as follows: MXUS = species distributed only in Mexico and the United States (except for a few perhaps found in Canada); MXCA = species found only in Mexico and Central America; MXSA = species ranging from Mexico to South America; USCA = species ranging from the United States to Central America (except for a few perhaps found in the Antilles); and USSA = species ranging from the United States to South America.

Family	Number of non-endemic species	Distributional status				
		MXUS species (3)	MXCA species (4)	MXSA species (6)	USCA species (7)	USSA species (8)
Bufonidae	3	2	—	—	1	—
Craugastoridae	1	1	—	—	—	—
Eleutherodactylidae	1	1	—	—	—	—
Hylidae	3	2	—	—	1	—
Microhylidae	1	—	—	—	1	—
Ranidae	1	1	—	—	—	—
Scaphiopodidae	1	1	—	—	—	—
Total	**11**	**8**	—	—	**3**	—
Anguidae	2	2	—	—	—	—
Dactyloidae	1	—	1	—	—	—
Phrynosomatidae	3	2	1	—	—	—
Scincidae	1	1	—	—	—	—
Teiidae	1	1	—	—	—	—
Subtotal	**8**	**6**	**2**	—	—	—
Boidae	1	—	—	1	—	—
Colubridae	8	4	1	2	1	—
Dipsadidae	4	2	1	—	—	1
Elapidae	1	1	—	—	—	—
Natricidae	3	1	—	—	2	—
Viperidae	3	3	—	—	—	—
Subtotals	**20**	**11**	**2**	**3**	**3**	**1**
Kinosternidae	1	1	—	—	—	—
Subtotal	**1**	**1**	—	—	—	—
Total	**29**	**18**	**4**	—	—	—
Sum Total	**40**	**26**	**4**	**3**	**6**	**1**

Potosí. The numbers of non-native species range from a low of three in Michoacán and Querétaro to a high of five in Guanajuato. The numbers of endemic species range from a low of 56 in Guanajuato to a high of 144 in Jalisco. Finally, the percentages of endemism range from a low of 40.1 in San Luis Potosí to a high of 66.0 in Michoacán. The average proportion of endemism in these five states is 55.8. Interestingly, the herpetofauna of Guanajuato is the smallest of those in the five states, but the percentage of endemism (55.4) is very close to that of the average for the five states (55.8).

Principal Environmental Threats

The state of Guanajuato is located in a highly commercialized region of Mexico, and this geographic entity connects the central portion of the country with the northern states. Guanajuato also encompasses an agro-industrial belt, beginning in the southern portion in Celaya, extending toward the northwest to the city of León, and toward the north to connect with the state of Aguascalientes, which represent the direction to the United States. Consequently, this area of Guanajuato also has a large number of people, constituting approximately 70% of the population. Unfortunately, because of these characteristics, significant impacts are seen on the flora and fauna of this area. Included among these organisms are the amphibians and reptiles, many of which tend to be more vulnerable to human-related activities. The effects of these factors can be noticed on the diversity and distribution of the herpetofauna across the state. For example, ongoing human activities in the last three decades have reduced significantly the original vegetation to isolated patches within a matrix

Table 10. Comparison of the numbers of endemic, non-endemic, and non-native species, and the percentage of endemism for Guanajuato, Mexico, and the states that surround it.

State	Total herpetofauna	Endemic species	% Endemism	Non-endemic species	Non-native species
Guanajuato	101	56	55.4	40	5
Jalisco	223	144	64.6	75	4
Michoacán	215	142	66.0	70	3
Querétaro	130	67	51.5	60	3
San Luis Potosí	182	73	40.1	105	4

Fig. 11. Agricultural activity takes place all over the state, but particularly in the south-central region. This image shows agroecosystems with secondary vegetation and remnants of low tropical forest in the vicinity of Urirero, Salvatierra, where seasonal crops are grown with the use of fertilizers and pesticides. *Photo by Adrian Leyte-Manrique.*

Fig. 12. This image taken in San Nicolás de los Agustinos, Municipio de Salvatierra, shows solid wastes which are a byproduct of industrial activities. A worn-out tire, empty bottles, and used cans of insecticides and fertilizers can be observed in the Lerma River in the southeastern portion of the state. *Photo by Adrian Leyte-Manrique.*

of cornfields, industrial parks, and continuous housing developments, particularly in the south-central portion of the state. However, Guanajuato is diverse with respect to all the sources that threaten its herpetofauna. Although the south-central region is presumably the most impacted, forestry and livestock activities have been intensive and continuous in the northern and northwestern portions of the state. In the southwest, however, agriculture is the most important factor, particularly the agave fields that involve considerable amounts of land that used to contain the native vegetation. Additionally, the pollution of streams, reservoirs, and the Lerma River (including its tributaries) are affecting populations of aquatic and semi-aquatic herpetofauna. Given the current situation, the herpetofauna of Guanajuato is represented by populations that are subjected to conditions impacted by five key human activities.

Agriculture. This activity takes place in approximately 70 to 80% of the state. In particular, fields are present in the south-central region, where the main crops traditionally have been corn, sorghum, and wheat, as well as legumes and other vegetables. Over the last five years, barley also has become an important crop, due to beer production by large companies such as Heineken (INEGI 2021). Traditional agricultural systems (seasonal) also are involved, but in smaller proportions, since these products are primarily produced for local consumption when compared to systems with intense irrigation. The latter systems have involved significant loss of the native vegetational cover (low tropical deciduous forest and scrub) and therefore, the loss of important shelter, feeding, and reproduction sites for amphibians and reptiles (Leyte-Manrique 2021). For instance, the distributions of frog species such as *Lithobates neovolcanicus*, *Dryophytes eximius*, and *D. arenicolor*, and the toads *Anaxyrus*

Fig. 13. Forestry activities inevitably result in the loss of vegetation cover. This image from El Varal, Guanajuato, shows patches of pine-oak forest. Trees are removed for construction and the production of charcoal. Currently, a reforestation program is being implemented at this site. *Photo by Adrian Leyte-Manrique.*

compactilis, *A. punctatus*, and *Incilius occidentalis* have decreased considerably, as indicated by fewer observations of these species in the past six years, especially in the south-central region of the state (Leyte-Manrique 2021). The pollution of reproduction sites for amphibians is associated with agricultural activity, due to the excessive use of chemicals in insecticides, herbicides, and fertilizers. Additionally, increasing ambient temperatures are reducing viable habitats (Corral et al. 2007; Guanajuato Produce 2022) due to the higher evaporation rates of seasonal ponds. With regards to reptiles, negative cultural perceptions have resulted in the indiscriminate killing of harmless species, such as the snakes *Pituophis deppei*, *Masticophis mentovarius*, and *Drymarchon melanurus*, locally known as Cencuate, Chirrionera, and Limpia Campos, respectively. Other snake species that also are affected include *Conopsis*

No. 17. *Conopsis nasus* (Günther, 1858). The Long-nosed Spotted Earthsnake ranges from the Sierra Madre Occidental of southern Chihuahua southward and eastward through much of the Mexican Plateau, occurring in the states of Chihuahua, Durango, Sinaloa, Zacatecas, Aguascalientes, San Luis Potosí, Jalisco, Michoacán, Guanajuato, Querétaro, Estado de México, Morelos, Distrito Federal, Hidalgo, and Puebla (Heimes 2016). This individual came from Guayabo de Santa Rita, in the municipality of Manuel Doblado. Wilson et al. (2013a) ascertained its EVS as 11, placing it in the lower portion of the medium vulnerability category. IUCN has assessed its conservation status as Least Concern, but SEMARNAT has not evaluated this species. *Photo by Adrian Leyte-Manrique.*

No. 18. *Drymarchon melanurus* (Duméril, Bibron, and Duméril, 1854). The Black-tailed Cribo is distributed "from south-central Texas, USA, on the Atlantic versant and from southern Sonora, Mexico, on the Pacific versant to northern Venezuela and northwestern Peru…It also occurs on the Islas Tres Marías, Nayarit, Mexico, and on the Islas de la Bahía and Isla del Tigre, Honduras" (McCranie 2011: 114). This individual was found in Área Natural Protegida Las Musas, in the municipality of Manuel Doblado. Wilson et al. (2013a) determined its EVS as 6, placing it in the middle of the low vulnerability category. IUCN has established its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Adrian Leyte-Manrique.*

No. 19. *Lampropeltis polyzona* (Cope, 1861). The Mexican Milksnake "ranges on the Pacific side from southern Sonora south to Guerrero, and across the southern part of the Mexican Plateau eastward to Veracruz and northern Oaxaca" (Heimes 2016: 89). This individual came from Janicho, in the municipality of Salvatierra. Mata-Silva et al. (2015) judged its EVS as 11, placing it in the lower portion of the medium vulnerability category. IUCN and SEMARNAT have not evaluated this species. *Photo by Adrian Leyte-Manrique.*

Fig. 20. *Masticophis mentovarius* (Duméril, Bibron, and Duméril, 1854). The Neotropical Whipsnake is distributed on the Pacific versant from Sonora and on the Atlantic versant from Tamaulipas south to Colombia and Venezuela. Its vertical distribution extends from near sea level to around 2,100 m (Johnson 1977, 1982 cited in Heimes 2016). This individual came from El Copal, in the municipality of Irapuato. Wilson et al. (2013a) ascertained its EVS as 6, placing it in the middle portion of the low vulnerability category. IUCN has not evaluated its conservation status, but SEMARNAT has assessed it as Threatened (A). *Photo by Adrian Leyte-Manrique.*

Fig. 14. Cows feeding in the vicinity of El Garbanzo, Irapuato, Guanajuato. Livestock production is common in the southeastern, south-central, and western portions of the state toward the Sierra Gorda. Cows can trample tadpoles (e.g., of *Anaxyrus compactilis*) living in the pools formed in these areas, consequently increasing the mortality rate of this amphibian developmental stage. (a) Cows feeding on grass, (b) an individual of *A. compactilis*. *Photo by Adrian Leyte-Manrique.*

lineata, *C. nasus*, *Trimorphodon tau*, and *Lampropeltis polyzona*, with the last species usually being mistaken for the venomous coralsnake *Micrurus tener*. With respect to turtles, the pollution of bodies of water, uncontrolled collection of individuals, and the presence of highly traveled roads contribute to the continuous decimation of local populations of *Kinosternon* (Leyte-Manrique 2021b).

Industrial activity. At the national level, Guanajuato is well known for its industrial sector. This includes vehicle assembly and the production of vehicle parts by companies such as Honda in the south (municipality of Celaya), Mazda in Silao, Toyota in Apaseo El Alto, and Volkswagen near the capital in the Celaya-León belt. Another large-scale activity is the production of agro-industrial chemicals, such as fertilizers, insecticides, and herbicides, particularly in the south-central region of the state. Likewise, the textile and fur industries are major activities taking place in the northwestern portion, in the municipality of León. Not surprisingly, all of these large-scale activities contribute significantly to the pollution of water bodies. Guanajuato contains 29 reservoirs that are important for fish farming and agriculture (Walter and Brooks 2009). One of the most important water sources is Laguna Yuriria, a natural protected area considered as a RAMSAR site due to its high bird diversity and abundance of amphibians and reptiles, such as *Lithobates montezumae* (POEGG 2005). All of the waste generated by these industrial businesses is discarded in these water sources in liquid and solid forms in both dams and rivers, particularly the Río Lerma, which transects the southeastern and northwestern regions of the state and runs through the industrial belt and the most populated region of the state. The flora and fauna present in reservoirs such as La Purísima have been affected significantly by the vehicle-related industries, but also by intense water extraction to satisfy the needs of nearby cities such as Guanajuato and Irapuato. Furthermore, nearby farming activities and recreational events, such as nautical regattas, also have an impact on these sites. All of these processes affect amphibians more directly, since species such as *Lithobates montezumae*, *L. megapoda*, and *L. neovolcanicus*, require water for accomplishing their reproductive cycles and their presence in La Purísima appears to be less evident (Leyte-Manrique et al. 2015). Conversely, it is encouraging to have a natural protected area such as Cuenca La Esperanza that provides protection to the herpetofauna present in the central portion of the state where reptiles, particularly snakes, seem to be more abundant (Instituto de Ecología del Estado de Guanajuato 1998).

Forestry. The exploitation of forests is regulated in the north, and this activity also takes place inside natural protected areas such as Cuenca La Esperanza, Sierra de Lobos, Sierra de los Agustinos, Sierra de Pénjamo, and Reserva de la Biosfera Sierra Gorda-Guanajuato (Ortiz-Mantilla et al. 2022). The exploitation of trees such as conifers and oaks is important in the state (INANPEG 2020). Although the extraction of lumber is regulated in the cold forests of the state, this is not the case for unprotected areas with low tropical deciduous forest. The latter forests experience illegal exploitation associated with the production of wood and charcoal, and the removal of vegetation for increasing housing development, as well as livestock and agricultural activities. For instance, the natural protected area Cerro de Arandas, in the municipality of Irapuato, has a low diversity of amphibians and reptiles likely due to the loss of native vegetation, even though this area has a management program. The herpetofauna of this area is forced to adapt

Fig. 15. Mining activity in Guanajuato takes place primarily in two areas, the city of Guanajuato and the Sierra Gorda (Reserva de la Biosfera Sierra Gorda-Guanajuato) in the municipality of Xichú. In general, the productivity in the city of Guanajuato is low, and only remnants of minerals were being extracted by 2013 in the Sierra Gorda. The pollution resulting from this activity, however, is evident in the air, soil, and water. (a) the mining area in the east, (b) an individual of *Lithobates berlandieri* found dead in a stream within the mining area, and tadpoles in a pool. *Photo by Adrian Leyte-Manrique.*

to the surrounding agroecosystems, especially during the dry season. Amphibians such as *Dryophytes arenicolor* and *D. eximius*, the snakes *Conopsis nasus*, *Masticophis mentovarius*, and *Senticolis triaspis*, and the turtle *K. integrum* have been recorded in agricultural areas near the city of Irapuato (Leyte-Manrique et al. 2021).

Livestock. This activity is more common in the northwestern and southwestern parts of the state, such as in the Sierra Gorda and the municipality of Manuel Doblado, where production is mostly at the regional and state levels. Observations indicate that the most visible impact of this activity is on populations of frogs and toads that use seasonal water sources for reproduction. At these sites, horses and cows can step on the eggs and tadpoles of these amphibians, and the toads *Anaxyrus compactilis* and *Spea multiplicata* are the species most commonly affected (Leyte-Manrique 2018). The same situation is expected to exist in other parts of the state that remain unstudied.

Mining. This activity is of great significance in the municipalities of Guanajuato and Xichú, in the northern portion of the state. One consequence of mining is the loss of native arboreal vegetation. Additionally, a high concentration of residues, such as lead and silver, eventually reach streams and ponds and affect a variety of aquatic organisms, including fish, amphibians, and freshwater turtles. Although the actual effect of this process on amphibians has not been examined, we assume that it is impacting the health and survival of the eggs and larval stages (Leyte-Manrique and Dominguez-Laso 2014; A. Leyte-Manrique, pers. obs.). Additionally, it is noteworthy that the impacts of mining on the populations of salamanders have been poorly studied, as we are aware of few salamander records from regions that are well known for their mining activity, such as Guanajuato and Xichú. Species such as *Isthmura bellii*, *Aquiloeurycea cephalica*, and *Ambystoma velasci* have been reported from these areas. Regarding *A. velasci*, there is information on its ecology and reproduction in Xichú, and it was determined that one of the main factors affecting its survival is the pollution of their aquatic

habitats by phosphates and other chemicals used in agriculture. Additionally, these organisms are unlawfully collected and sold on the black market (Leyte-Manrique et al. 2016; De la Cruz-Beltrán et al. 2018).

Conservation Status

This study employed the three systems of conservation assessment that were used in all the entries in the Mexican Conservation series (see above), i.e., the systems of SEMARNAT (2010), the IUCN Red List (http://www.iucnredlist.org), and the EVS (Wilson et al. 2013a, b). The assessments from these three systems were updated as necessary.

The SEMARNAT System

Torres-Hernández et al. (2021: 117) stated that "the SEMARNAT system for assessing conservation status was developed and implemented by the Secretaría del Medio Ambiente y Recursos Naturales of the federal government of Mexico (SEMARNAT 2010)," and the status ratings for the native herpetofaunal species in Guanajuato are provided in Table 7 and summarized in Table 11. Three categories of assessment are established in the SEMARNAT system, including Endangered (P), Threatened (A), and Under Special Protection (Pr); and those species that are not assessed are allocated to a "No Status" (NS) category (Tables 7 and 11).

As in previous MCS entries, one frequently asked question is why so few species in any given state herpetofauna have been assessed using this system. Perhaps the personnel at SEMARNAT favor listing species endemic to Mexico and not those that also are shared with either the USA or countries in Central America (i.e., the non-endemics). If so, then it might be possible to ascertain an answer to this question by comparing the SEMARNAT assignments in the endemic and non-endemic categories. In an effort to determine whether such a bias might exist, these comparisons are shown in Table 12. The data in Table 12 demonstrate that of the 96 total native species in Guanajuato, only 44 species (45.8%) have been assessed to date, with 16 placed in the Threatened (A) category and 28 in the

Table 11. SEMARNAT categorizations for herpetofaunal species in Guanajuato, Mexico, arranged by families. Non-native species are excluded.

Family	Number of species	SEMARNAT categorization			
		Endangered (P)	Threatened (A)	Special protection (Pr)	No status (NS)
Bufonidae	5	—	—	—	5
Craugastoridae	2	—	—	—	2
Eleutherodactylidae	3	—	—	2	1
Hylidae	6	—	1	—	5
Microhylidae	1	—	—	—	1
Ranidae	5	—	1	3	1
Scaphiopodidae	1	—	—	—	1
Subtotal	**23**	**—**	**2**	**5**	**16**
Ambystomatidae	1	—	—	1	—
Plethodontidae	2	—	2	—	—
Subtotal	**3**	**—**	**2**	**1**	**—**
Total	**26**	**—**	**4**	**6**	**16**
Anguidae	4	—	—	3	1
Dactyloidae	2	—	—	—	2
Phrynosomatidae	10	—	1	1	8
Scincidae	3	—	—	2	1
Sphenomorphidae	1	—	1	—	—
Teiidae	1	—	—	—	1
Xantusiidae	2	—	—	2	—
Subtotal	**23**	**—**	**2**	**8**	**13**
Boidae	1	—	—	—	1
Colubridae	18	—	5	2	11
Dipsadidae	11	—	—	4	7
Elapidae	1	—	—	—	1
Natricidae	9	—	5	1	3
Viperidae	5	—	—	5	—
Subtotal	**45**	**—**	**10**	**12**	**23**
Kinosternidae	2	—	—	2	—
Subtotal	**2**			**2**	**—**
Total	**70**	**—**	**12**	**22**	**36**
Sum total	**96**	**—**	**16**	**28**	**52**

No. 21. *Pituophis deppei* (Duméril, 1853). The Mexican Bullsnake occurs in the states of Aguascalientes, Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Nuevo León, Oaxaca, Puebla, San Luis Potosí, Querétaro, Tlaxcala, Veracruz, Zacatecas, and Ciudad de México (Ramírez-Bautista et al. 2014). This individual was encountered in the municipality of Mineral El Chico. Wilson et al. (2013a) calculated its EVS as 14, placing it at the lower limit of the high vulnerability category. IUCN has determined its conservation status as Least Concern, and SEMARNAT as Threatened (A). *Photo by Adrian Leyte-Manrique.*

No. 22. *Salvadora bairdi* (Jan, 1860). Baird's Patch-nosed Snake occurs throughout much of the Sierra Madre Occidental and the Mexican Plateau, ranging from southwestern Chihuahua and adjacent eastern Sonora to the Transverse Volcanic Cordillera as far south as southeastern Puebla (Valle de Tehuacán) and northwestern Oaxaca (Heimes 2016). This individual came from Campamento las Palomas, in the municipality of Guanajuato. Wilson et al. (2013a) estimated its EVS as 15, placing it in the lower portion of the high vulnerability category. IUCN has assessed its conservation status as Least Concern, and SEMARNAT as a species of Special Protection (Pr). *Photo by Adrian Leyte-Manrique.*

No. 23. *Trimorphodon tau* (Cope, 1869). The Mexican Lyre Snake is widely distributed along the coastal slopes and foothills of the Sierra Madre Oriental, the Sierra Madre Occidental, and the Sierra Madre del Sur, and across the Mexican Plateau and the Mesa de Oaxaca (Heimes 2016). This individual was photographed in the vicinity of Aldama, in the municipality of Guanajuato. Wilson et al. (2013a) determined its EVS as 13, placing it at the upper limit of the medium vulnerability category. IUCN evaluated its conservation status as Least Concern, but SEMARNAT has not listed this species. *Photo by Samuel Cadena-Rico.*

No. 24. *Thamnophis melanogaster* (Peters, 1864). The Black-bellied Gartersnake is a Mexican endemic occurring from "southwestern Chihuahua and adjacent Sonora south-southeastward to the Valley of Mexico, western Querétaro, and southern San Luis Potosí" (Lemos-Espinal and Dixon 2013). This individual came from San Nicolás de los Agustinos, in the municipality of Salvatierra. Wilson et al. (2013a) calculated its EVS as 15, placing it in the lower portion of the high vulnerability category. IUCN has evaluated its conservation status as Endangered, and SEMARNAT as Threatened (A). *Photo by Adrian Leyte-Manrique.*

Table 12. Comparison of SEMARNAT and distributional categorizations for the Guanajuato herpetofauna. Non-native species are excluded.

Distributional category	SEMARNAT category			
	Threatened (A)	Special Protection (Pr)	No Status (NS)	**Total**
Non-endemic species (NE)	4	9	27	**40**
Country-endemic species (CE)	12	19	25	**56**
Total	**16**	**28**	**52**	**96**

Special Protection (Pr) category. No species are placed in the Endangered (P) category. The data indicate that of the 16 species allocated to the Threatened (A) category, four (25.0%) are non-endemic species and 12 (75.0%) are country endemics (Table 12). Of the 28 species placed in the Special Protection (Pr) category, nine (32.1%) are non-endemics and 19 (67.9%) are country endemics. Apparently, some favor has been given to the assessment of country endemic species. Conversely, however, since 52 (54.2%) of the 96 species that could be allocated using the SEMARNAT categories have not been assessed, the conservation assessment of the Guanajuato herpetofauna using this system is seriously deficient and of little value in our effort to determine the conservation status of the herpetofauna of this state.

The IUCN System

The IUCN system of conservation assessment is applied primarily to vertebrate animals and flowering plants, leaving the conservation status of the major swath of organisms, including prokaryotes, algae, fungi, and invertebrates largely unassessed. This system has been applied to amphibians and reptiles to some degree, and it

Table 13. IUCN Red List categorizations for herpetofaunal families in Guanajuato, Mexico. Non-native species are excluded. The shaded columns to the left are the "threat categories," and those to the right the categories for which too little information on conservation status exists to allow the taxa to be placed in any other IUCN category, or they have not been evaluated.

Family	Number of species	IUCN Red List categorization						
		Critically Endangered	Endangered	Vulnerable	Near Threatened	Least Concern	Data Deficient	Not Evaluated
Bufonidae	5	—	—	—	—	4	—	1
Craugastoridae	2	—	—	—	—	1	1	—
Eleutherodactylidae	3	—	—	2	—	1	—	—
Hylidae	6	—	—	—	1	5	—	—
Microhylidae	1	—	—	—	—	1	—	—
Ranidae	5	—	—	1	1	3	—	—
Scaphiopodidae	1	—	—	—	—	1	—	—
Subtotal	**23**	—	—	**3**	**2**	**16**	1	**1**
Ambystomatidae	1	—	—	—	—	1	—	—
Plethodontidae	2	—	—	1	1	—	—	—
Subtotal	**3**	—	—	**1**	**1**	**1**	—	—
Total	**26**	—	—	**4**	**3**	**17**	1	**1**
Anguidae	4	—	—	1	—	3	—	—
Dactyloidae	2	—	—	—	—	1	—	1
Phrynosomatidae	10	—	—	—	—	10	—	—
Scincidae	3	—	—	1	—	2	—	—
Sphenomorphidae	1	—	—	—	—	1	—	—
Teiidae	1	—	—	—	—	1	—	—
Xantusiidae	2	—	—	1	—	1	—	—
Subtotal	**23**	—	—	**3**	—	**19**	—	**1**
Boidae	1	—	—	—	—	—	—	1
Colubridae	18	—	—	—	—	16	—	2
Dipsadidae	11	—	—	—	—	5	4	2
Elapidae	1	—	—	—	—	1	—	—
Natricidae	9	—	1	2	—	6	—	—
Viperidae	5	—	—	—	—	5	—	—
Subtotal	**45**	—	**1**	**2**	—	**33**	**4**	**5**
Kinosternidae	2	—	—	—	—	2	—	—
Subtotal	**2**	—	—	—	—	**2**	—	—
Total	**70**	—	**1**	**5**	—	**54**	**4**	**6**
Sum total	**96**	—	**1**	**9**	**3**	**71**	**5**	**7**
Category total	**96**	**10**			**74**		**12**	

Table 14. Environmental Vulnerability Scores (EVS) for the herpetofaunal species in Guanajuato, Mexico, arranged by family. The shaded area on the left encompasses low vulnerability scores, and the one on the right indicates the high vulnerability scores. Non-native species are excluded.

Family	Number of species	Environmental Vulnerability Score (EVS)														
		3	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Bufonidae	5	1		1	1					1			1			
Craugastoridae	2						1					1				
Eleutherodactylidae	3									1					1	1
Hylidae	6	1				1	1	1	1	1						
Microhylidae	1		1													
Ranidae	5					1					1	2	1			
Scaphiopodidae	1				1											
Subtotal	**23**	**2**	**1**	**1**	**2**	**2**	**2**	**1**	**1**	**3**	**1**	**3**	**2**		**1**	**1**
Ambystomatidae	1								1							
Plethodontidae	2										1		1			
Subtotal	**3**								**1**		**1**		**1**			
Total	**26**	**2**	**1**	**1**	**2**	**2**	**2**	**1**	**2**	**3**	**2**	**3**	**3**		**1**	**1**
Anguidae	4				1							1	1	1		
Dactyloidae	2						1					1				
Phrynosomatidae	10			1				1	1	1	3	2	1			
Scincidae	3								1		1				1	
Sphenomorphidae	1										1					
Teiidae	1							1								
Xantusiidae	2											1	1			
Subtotal	**23**			**1**	**1**		**1**	**2**	**2**	**1**	**5**	**5**	**3**	**1**	**1**	
Boidae	1								1							
Colubridae	18			1	3		1	1		3		5	2	2		
Dipsadidae	11		1		1		1	1	1		1	2	1	2		
Elapidae	1									1						
Natricidae	9					2	1			1			1	4		
Viperidae	5						1	1		1					2	
Subtotal	**45**		**1**	**1**	**4**	**2**	**4**	**3**	**2**	**6**	**1**	**7**	**4**	**8**	**2**	
Kinosternidae	2								1	1						
Subtotal	**2**								**1**	**1**						
Total	**70**		**1**	**2**	**5**	**2**	**5**	**5**	**5**	**8**	**6**	**12**	**7**	**9**	**3**	
Sum total	**96**	**2**	**2**	**3**	**7**	**4**	**7**	**6**	**7**	**11**	**8**	**15**	**10**	**9**	**4**	**1**
Category total	**96**	**31**							**41**				**24**			

Table 15. Comparison of Environmental Vulnerability Scores (EVS) and IUCN categorizations for the members of the herpetofauna of Guanajuato, Mexico. Non-native species are excluded. The shaded area at the top encompasses the low vulnerability category scores, and the shaded area at the bottom indicates the high vulnerability category scores.

EVS	IUCN category							Total
	Critically Endangered	**Endangered**	**Vulnerable**	**Near Threatened**	**Least Concern**	**Data Deficient**	**Not Evaluated**	
3	—	—	—	—	1	—	1	2
4	—	—	—	—	2	—	—	2
5	—	—	—	—	3	—	—	3
6	—	—	—	—	6	—	1	7
7	—	—	—	—	4	—	—	4
8	—	—	—	—	5	—	2	7
9	—	—	—	1	5	—	—	6
10	—	—	—	—	6	—	1	7
11	—	—	—	—	9	—	2	11
12	—	—	1	—	6	1	—	8
13	—	—	1	1	12	1	—	15
14	—	—	1	1	7	1	—	10
15	—	1	3	—	3	2	—	9
16	—	—	2	—	2	—	—	4
17	—	—	1	—	—	—	—	1
Total	—	**1**	**9**	**3**	**71**	**5**	**7**	**96**

No. 25. *Crotalus aquilus* (Klauber, 1952). The Dusky Rattlesnake is found "from the region of Lake Chapala, Jalisco, eastward through Michoacán, Guanajuato, Querétaro, central San Luis Potosí, and southeastward through northern Hidalgo and northwestern Veracruz" (Lemos-Espinal and Dixon 2013: 249). This individual was encountered in Cuenca Baja del Río Temascatio, in the municipality of Irapuato. Wilson et al. (2013a) ascertained its EVS as 16, placing it in the middle portion of the high vulnerability category. IUCN has assessed this species as Least Concern, and SEMARNAT as in the Special Protection (Pr) category. *Photo by Mará Fernanda Rodríguez-Gutiérrez.*

No. 26. *Crotalus molossus* (Baird and Girard, 1853). The Black-tailed Rattlesnake occurs from northwestern Arizona and southwestern New Mexico on the west, southward along the Pacific Coastal Plain, Sierra Madre Occidental, and Mexican Plateau to Michoacán, and from Coahuila and Nuevo León on the east, southward along the Sierra Madre Oriental and Mexican Plateau to northwestern Oaxaca (Anderson and Greenbaum 2012). This individual came from El Garbanzo, in the municipality of Irapuato. Wilson et al. (2013a) calculated its EVS as 8, placing it in the upper portion of the low vulnerability category. IUCN has determined its conservation status as Least Concern, and SEMARNAT as a species of Special Protection (Pr). *Photo by Adrian Leyte-Manrique.*

consists of six categories (Table 13), including three so-called "threat categories" of Critically Endangered (CR), Endangered (EN), and Vulnerable (VU). Two categories of so-called "lesser risk," i.e., Near Threatened (NT) and Least Concern (LC), also are involved. A sixth category, called Data Deficient (DD) is established, and it is assigned to species which lack sufficient information for placement into another category. Finally, another category of Not Evaluated (NE) is used here for species that the IUCN has not evaluated thus far. Two other categories exist for species thought to be either Extinct (EX) or Extinct in the Wild (EW), but these are seldom applicable to herpetofaunal species.

The data for allocating the species that comprise the Guanajuato herpetofauna are shown in Table 7 and summarized in Table 13. The data in Table 13 demonstrate that only 10 species are allocated to two of the three "threat categories." A single species (*Thamnophis melanogaster**) is placed in the Endangered (EN) category, and nine species are in the Vulnerable (VU) category (*Eleutherodactylus angustidigitorum**, *E. verrucipes**, *Lithobates megapoda**, *Isthmura bellii**, *Abronia taeniata**, *Plestiodon dugesii**, *Lepidophyma gaigeae**, *Adelophis copei**, and *Thamnophis scaliger**). These 10 species are all country endemics. No species are allocated to the Critically Endangered (CR) category. Of the 74 species placed in the "lesser risk" categories, three country endemics (*Rheohyla miotympanum**, *Lithobates neovolcanicus**, and *Aquiloeurycea cephalica**) are considered as Near Threatened (NT), and 71 species are classified as Least Concern (LC). The five Data Deficient (DD) species are *Craugastor occidentalis**, *Geophis latifrontalis**, *G. petersii**, *Hypsiglena tanzeri**, and *Rhadinaea gaigeae**. As with the EN and VU species, all of these five species are country endemics.

No. 27. *Kinosternon integrum* (Le Conte, 1854). The Mexican Mud Turtle is endemic to Mexico, and it is distributed from central Sonora to Oaxaca, as well as from southwestern Tamaulipas and the central and southern portions of the Mexican Plateau (Lemos-Espinal and Dixon 2013). This individual was found at Presa La Galera, in the municipality of Abasolo. Wilson et al. (2013a) determined its EVS as 11, placing it in the lower portion of the medium vulnerability category. IUCN has assessed its conservation status as Least Concern, and SEMARNAT has placed it in the Special Protection (Pr) category. *Photo by Adrian Leyte-Manrique.*

Seven species have not been evaluated by the IUCN, as follows: *Rhinella horribilis*, *Norops sericeus*, *Boa imperator*, *Lampropeltis polyzona**, *Oxybelis microphthalmus*, *Hypsiglena jani*, and *Leptodeira*

Table 16. Environmental Vulnerability Scores (EVS) for members of the herpetofauna of Guanajuato, Mexico, that are allocated to the IUCN Data Deficient category. * = country endemic.

Taxon	Environmental Vulnerability Score (EVS)			
	Geographic distribution	Ecological distribution	Reproductive mode/Degree of persecution	Total score
*Craugastor occidentalis**	5	4	4	13
*Geophis latifrontalis**	5	7	2	14
*Geophis petersii**	5	8	2	15
*Hypsiglena tanzeri**	5	8	2	15
*Rhadinaea gaigeae**	5	5	2	12

septentrionalis. Only one of these seven species is a country endemic, and the others are relatively widespread non-endemic species (two are NE3 species, and one each are NE4, NE6, NE7, and NE8 species).

The 71 species allocated to the LC category comprise 74.0% of the 96 native species in Guanajuato. Thirty-seven of these 71 species (52.1%) are country endemics and the remaining 34 (47.9%) are non-endemics. Given that almost three-quarters of the herpetofauna has been judged as Least Concern by using the IUCN system of conservation assessment, it might seem that the herpetofauna of Guanajuato is in reasonably good shape from a conservation perspective. However, since such a status has not been the case in the other MCS studies, this assumption is subjected to further analysis using the EVS system.

The EVS System

Initially, the Environmental Vulnerability Score (EVS) system of conservation assessment was developed to examine the herpetofauna of Honduras (Wilson and McCranie 2003), inasmuch as the population status of species in this herpetofauna was not sufficiently understood for assessment using the IUCN system. Since that time, the EVS has been applied to all of the Mexican and Central American herpetofaunas (Wilson et al. 2013a,b; Johnson et al. 2015a), as well as all 14 of the previously-published Mexican Conservation Series (MCS) studies (see above). In addition, this system is becoming increasingly applied in studies by other workers on the Mexican herpetofauna, especially by J. Lemos-Espinal and his co-authors.

In this study, we calculated the EVS values for the 96 native species of the Guanajuato herpetofauna, and they are shown in Table 7 and summarized in Table 14. The EVS values range from 3 to 17, three fewer than the total theoretical range of values (3–20). The most frequent values (i.e., those associated with 10 or more species) are 11 (11 species), 13 (15), and 14 (10). Note that these three values apply to 36 of the 96 native species in Guanajuato. The lowest score of 3 was determined only for two anuran species (*Rhinella horribilis* and *Smilisca baudinii*). The highest value of 17 was applied to only a single anuran species (*Eleutherodactylus angustidigitorum**).

As with all the previous MCS studies, the EVS values were grouped into the categories of low (3–9), medium (10–13), and high (14–17) vulnerability. Based on this categorization, the resulting figures increase from low vulnerability (31 species) through medium (41), and then decrease to high vulnerability (24). In both of these states, the native herpetofaunas consist essentially of non-endemic and country endemic species, with the exception being that Querétaro harbors a single state endemic, i.e., *Sceloporus exsul*. In the Querétaro herpetofauna, there are 60 non-endemics and 67 country endemics, while the respective figures in Guanajuato are 40 and 56.

In an effort to assess how the IUCN ratings relate to those for the EVS, the categorizations of these two systems are compared in Table 15. Only 10 of the 24 high vulnerability species (41.7%) are allocated to the IUCN "threat categories." At the other extreme, 31 of the low vulnerability species (by EVS) account for only 43.7% of the 71 LC species (by IUCN). Thus, as generally seen in the other MCS studies, there is little correspondence between the conservation evaluations provided by the IUCN and the EVS categorizations.

Table 17. Environmental Vulnerability Scores (EVS) for members of the herpetofauna of Guanajuato, Mexico, that are currently Not Evaluated (NE) by the IUCN. Non-native taxa are excluded. * = country endemic.

Taxon	Environmental Vulnerability Score (EVS)			
	Geographic distribution	Ecological distribution	Reproductive mode/Degree of persecution	Total score
Rhinella horribilis	1	1	1	3
Norops sericeus	2	3	3	8
Boa imperator	3	1	6	10
*Lampropeltis polyzona**	1	3	5	9
Oxybelis microphthalmus	2	6	3	11
Hypsiglena jani	1	3	2	6
Leptodeira septentrionalis	2	2	4	8

Table 18. Environmental Vulnerability Scores (EVS) for members of the herpetofauna of Guanajuato, Mexico, that are assigned to the IUCN Least Concern (LC) category. Non-native taxa are excluded. * = country endemic.

Taxon	Environmental Vulnerability Score (EVS)			
	Geographic distribution	Ecological distribution	Reproductive mode/Degree of persecution	Total score
*Anaxyrus compactilis**	5	8	1	14
Anaxyrus punctatus	1	3	1	5
Incilius nebulifer	1	4	1	6
*Incilius occidentalis**	5	5	1	11
Craugastor augusti	2	2	4	8
Eleutherodactylus guttilatus	2	5	4	11
Dryophytes arenicolor	2	4	1	7
*Dryophytes eximius**	5	4	1	10
*Dryophytes plicata**	5	5	1	11
Smilisca baudinii	1	1	1	3
Smilisca fodiens	2	5	1	8
Hypopachus variolosus	2	1	1	4
Lithobates berlandieri	4	2	1	7
*Lithobates montezumae**	5	7	1	13
*Lithobates spectabilis**	5	6	1	13
Spea multiplicata	1	4	1	6
*Ambystoma velasci**	5	4	1	10
*Barisia imbricata**	5	6	3	14
Gerrhonotus infernalis	5	5	3	13
Gerrhonotus liocephalus	2	1	3	6
*Norops nebulosus**	5	5	3	13
Holbrookia maculata	1	6	3	10
*Phrynosoma orbiculare**	5	4	3	12
*Sceloporus aeneus**	5	5	3	13
*Sceloporus dugesii**	5	5	3	13
Sceloporus grammicus	2	4	3	9
*Sceloporus minor**	5	6	3	14
*Sceloporus scalaris**	5	4	3	12
Sceloporus serrifer	2	1	3	6
*Sceloporus spinosus**	5	4	3	12
*Sceloporus torquatus**	5	3	3	11
Sceloporus variabilis	1	1	3	5
*Plestiodon lynxe**	5	2	3	10
Plestiodon tetragrammus	4	5	3	12
*Scincella silvicola**	5	4	3	12
Aspidoscelis gularis	2	4	3	9
*Lepidophyma occulor**	5	7	2	14
*Conopsis lineata**	5	6	2	13
*Conopsis nasus**	5	4	2	11
Drymarchon melanurus	1	1	4	6
Leptophis mexicanus	1	1	4	6
*Leptophis diplotropis**	5	5	4	14
Masticophis flagellum	1	3	4	8
Masticophis mentovarius	1	1	4	6
Masticophis schotti	4	5	4	13
Pantherophis emoryi	3	6	4	13
*Pituophis deppei**	5	5	4	14
*Pseudoficimia frontalis**	5	5	3	13
*Salvadora bairdi**	5	6	4	15
Senticolis triaspis	2	1	3	6
*Tantilla bocourti**	5	2	2	9
Tantilla rubra	2	1	2	5
*Trimorphodon tau**	5	4	4	13
Diadophis punctatus	1	1	2	4
*Geophis dugesii**	5	6	2	13
Geophis sartorii	2	2	5	9

Table 18 (continued). Environmental Vulnerability Scores (EVS) for members of the herpetofauna of Guanajuato, Mexico, that are assigned to the IUCN Least Concern (LC) category. Non-native taxa are excluded. * = country endemic.

Taxon	Environmental Vulnerability Score (EVS)			
	Geographic distribution	Ecological distribution	Reproductive mode/Degree of persecution	Total score
*Rhadinaea hesperia**	5	3	2	10
*Rhadinaea taeniata**	5	6	2	13
Micrurus tener	1	5	5	11
Storeria dekayi	1	4	2	7
*Storeria storerioides**	5	4	2	11
Thamnophis cyrtopsis	2	1	4	7
Thamnophis eques	2	2	4	8
*Thamnophis pulchrilatus**	5	6	4	15
*Thamnophis scalaris**	5	5	4	14
*Crotalus aquilus**	5	6	5	16
Crotalus atrox	1	3	5	9
Crotalus molossus	2	1	5	8
*Crotalus polystictus**	5	6	5	16
Crotalus scutulatus	2	4	5	11
Kinosternon hirtipes	2	5	3	10
*Kinosternon integrum**	5	3	3	11

As shown in previous MCS studies, the principal reason for the poor correspondence between the two systems of conservation evaluation is the large number of species allocated to the IUCN LC, DD, and NE categories. In the case of the Guanajuato herpetofauna, this applies to 83 of the 96 total native species (86.5%). Of these 83 species, five are allocated to the DD category (Table 16); one is an anuran and four are snakes. All five species are country endemics, and their EVS values range from 12 to 15. Leaving these five species in the DD category consigns them to a status of being ignored. In our opinion, the two species with EVS values of 12 (*Rhadinaea gaigeae**) and 13 (*Craugastor occidentalis**) should be placed in the NT category. The species with an EVS of 14 (*Geophis latifrontalis**) should be allocated to the VU category, and the two species with an EVS of 15 (*Geophis petersii** and *Hypsiglena tanzeri**) should be relegated to the EN category.

Seven species remain unassessed by the IUCN (Table 17). These species include one anuran, one lizard, and five snakes. Only one of these species (*Lampropeltis polyzona**) is a country endemic, and the remaining are non-endemics. Their EVS values range from three to 11. The six species with an EVS from 3 to 10 can be allocated to the LC category and the remaining species (*Oxybelis microphthalmus*), with an EVS of 11, should be placed in the NT category.

The highest number of species in the Guanajuato herpetofauna (71) is allocated to the LC category (Table 18). Comprising this group of 71 species are 16 anurans, one salamander, 19 lizards, 33 snakes, and two turtles. Of these species, 37 are country endemics and 34 are non-endemics. Their EVS values range from 3–16, just one less than the entire range for the Guanajuato herpetofauna (3–17). Thirty-two of these species have EVS scores from 3 to 10, and in our opinion, they can be retained in the Least Concern category. Twenty-seven species have EVS values ranging from 11 to 13, and thus they could be placed in the NT category. Seven species have an EVS of 14 and could be allocated to the VU category. The three species with an EVS of 15 (*Barisia imbricata**, *Salvadora bairdi**, and *Thamnophis pulchrilatus**) and the two species with an EVS of 16 (*Crotalus aquilus** and *C. polystictus**) should be allocated to the EN category.

Relative Herpetofaunal Priority

The concept of Relative Herpetofaunal Priority (RHP) was developed by Johnson et al. (2015a) in the MCS paper on the state of Chiapas. This method involves a simple means of ascertaining the relative conservation importance of the herpetofauna of any geographical entity (e.g., a physiographic region, a municipality, or a state), and consists of two parts: (1) determining the proportion of country endemic species (and in some

Table 19. Number of herpetofaunal species in three distributional status categories among the three physiographic regions of Guanajuato, Mexico. Rank is based on the number of country endemics.

Physiographic region	Distributional category			Total	Rank order
	Non-endemic	Country endemic	Non-native		
Central Plateau	23	36	1	60	3
Transmexican Volcanic Belt	27	43	4	74	1
Sierra Madre Oriental	38	37	—	75	2

Table 20. Number of herpetofaunal species in the three EVS categories among the three physiographic regions in Guanajuato, Mexico. Rank order is determined by the relative number of high EVS species. Non-native species are excluded.

Physiographic province	EVS category			Total	Rank order
	Low	Medium	High		
Central Plateau	18	27	14	59	3
Transmexican Volcanic Belt	20	31	18	69	1
Sierra Madre Oriental	27	32	15	74	2

cases, state endemic species) relative to the entire regional herpetofauna; and (2) calculating the absolute number of high EVS category species in each regional herpetofauna. The pertinent data for these two approaches are presented in Tables 19 and 20.

Based on the number of country endemic species in each of the three physiographic regions and the rank each region occupies (Table 19), this measure indicates that the most important region is, interestingly enough, the Transmexican Volcanic Belt with 43 country endemic species. In most cases, the Sierra Madre Oriental occupies the first rank in the states that encompass a portion of this biodiverse range, including Puebla (Woolrich-Piña et al. 2017), Hidalgo (Ramírez-Bautista et al. 2020), Veracruz (Torres-Hernández et al. 2021), and Querétaro (Cruz-Elizalde et al. 2022). In the case of Guanajuato, the likely reason for this shift in rank for the Sierra Madre Oriental is that the Transmexican Volcanic Belt segment is several times larger than the Sierra Madre Oriental segment.

Based on the relative numbers of high vulnerability species (Table 20), the first rank is occupied by the Transmexican Volcanic Belt, with 18 high vulnerability species out of a total of 69 native species (26.1%). The second rank is occupied by the Sierra Madre Oriental, with 15 high vulnerability species out of a total of 74 native species (20.3%). Finally, the third rank is held by the Central Plateau, with 14 high vulnerability species out of a total of 59 native species (23.7%).

The rankings based on the country endemic species numbers are the same as for the high vulnerability species numbers, i.e., first rank is the Transmexican Volcanic Belt; second rank is the Sierra Madre Oriental; and third rank is the Central Plateau. Thus, the Transmexican Volcanic Belt is the most important physiographic region because it contains the second highest number of native species (70), the highest number of country endemic species (43), and the highest number of high vulnerability species (18). As noted above, this result was a bit surprising, although the Sierra Madre Oriental herpetofauna, which was often was the most important in several other MCS studies, occupies the smallest amount of area in Guanajuato.

The 43 country endemic species in the TVB include 10 anurans, two salamanders, 30 squamates, and one turtle. The TVB also harbors 18 high vulnerability species (with their EVS scores in parentheses):

*Anaxyrus compactilis** (14)
*Eleutherodactylus angustidigitorum** (17)
*Lithobates megapoda** (14)
*Barisia imbricata** (14)
*Plestiodon dugesii** (16)
*Lampropeltis mexicana** (15)
*Leptophis diplotropis** (14)
*Pituophis deppei** (14)
*Salvadora bairdi** (15)
*Geophis petersi** (15)
*Hypsiglena tanzeri** (15)
*Adelophis copei** (15)
*Thamnophis melanogaster** (15)
*Thamnophis pulchrilatus** (15)
*Thamnophis scalaris** (14)
*Thamnophis scaliger** (15)
*Crotalus aquilus** (16)
*Crotalus polystictus** (16)

These 18 species include three anurans, two lizards, and 13 snakes. All of these species are country endemics and they have EVS values ranging from 14 to 17.

The Sierra Madre Oriental (rank two) contains 15 high vulnerability species:

*Eleutherodactylus angustidigitorum** (17)
*Eleutherodactylus verrucipes** (16)
*Aquiloeurycea cephalica** (14)
*Abronia taeniata** (15)
*Barisia imbricata** (14)
*Sceloporus minor** (14)
*Lepidophyma occulor** (14)
*Lampropeltis mexicana** (15)
*Pituophis deppei** (14)
*Salvadora bairdi** (15)
*Geophis latifrontalis** (14)
*Hypsiglena tanzeri** (15)
*Thamnophis pulchrilatus** (15)
*Thamnophis scalaris** (14)
*Crotalus aquilus** (16)

These 15 species include two anurans, one salamander, four lizards, and eight snakes. All 15 species are country endemics and are assigned EVS values from 14 to 17.

Finally, the Central Plateau (rank three) harbors 14 high vulnerability species:

*Anaxyrus compactilis** (14)
*Eleutherodactylus verrucipes** (16)
*Lithobates megapoda** (14)
*Barisia imbricata** (14)

*Sceloporus minor** (14)
*Leptophis diplotropis** (14)
*Pituophis deppei** (14)
*Salvadora bairdi** (15)
*Hypsiglena tanzeri** (15)
*Thamnophis melanogaster** (15)
*Thamnophis scalaris**
*Thamnophis scaliger** (15)
*Crotalus aquilus** (16)
*Crotalus polystictus** (16)

These 14 species include three anurans, two lizards, and nine snakes. All 14 species are country endemics and have EVS values ranging from 14 to 16.

Of the 101 species that comprise the Guanajuato herpetofauna (96 of which have calculable EVS), 24 are high vulnerability species and the proportions of these species in the three physiographic regions are as follows: TVB (75.0%), SMO (62.5%), and CP (58.3%). These data will be of considerable value in developing management plans for the protected areas in Guanajuato, as discussed in the next section.

Protected Areas in Guanajuato

Protected Areas and Worldview

Most humans appear to be afflicted with a social disease termed anthropocentrism, for which the symptoms arise from denying the reality of natural law. Briefly stated, life on Earth is entirely dependent on the functional interaction of the three abiotic spheres, i.e., the atmosphere, hydrosphere, and lithosphere. This relationship dates back to the origin of life on this planet, approximately 3.5 billion years ago. Since modern-day humans are socialized to support worldviews at odds with this reality, such a belief system has been the source of all current environmental problems. The most widespread worldviews adopted by humans are contrasted by Wilson and Lazcano (2019: 26), who promulgated the categorical ethical position that "what is good is defined in terms of what is right." Thus, these authors would argue that what is bad is defined in terms of what is wrong. Further, they argue, "What is right is that which enhances the survival of life on Earth" and "that which is wrong is that which compromises it." Their position, therefore, is that "with the right to enjoy life comes the responsibility to not endanger the lives of others" (Wilson and Lazcano 2019: 26).

Clearly, based on varying experiences, this view of life is not shared by most people. As noted by Miller (2006: 431), environmental worldviews are based on "how people think the world works, what they believe their environmental role in the world should be, and what they believe is right and wrong environmental behavior." Miller (2006: 432) identified three principal environmental worldviews: the Planetary Management Worldview, Stewardship Worldview, and Environmental Wisdom Worldview. The worldview adopted by the authors of this paper is characterized by the following ethical positions: (1) "we are a part of and totally dependent on nature and nature exists for all species"; (2) "resources are limited, should not be wasted, and are not all for us"; (3) "we should encourage earth-sustaining forms of economic growth and discourage earth-degrading forms"; and (4) "our success depends on learning how nature sustains itself and integrating such lessons from nature into the ways we think." Miller (2006: 431) also stated that "many people in today's industrial consumer societies have a planetary management worldview." This worldview, which clearly is at odds with our own, is based on the following ideas: (1) "we are apart from the rest of nature and can manage nature to meet our increasing needs and wants"; (2) "because of our ingenuity and technology we will not run out of resources"; (3) "the potential for economic growth is essentially unlimited"; and (4) "our success depends on how well we manage the earth's life-support systems mostly for our benefit."

The dangers associated with the Planetary Management Worldview are becoming more evident with the passing of time. Judging by the news of the day, climate change is becoming an issue that is more difficult to ignore than in the past. The latest (sixth) report of the Intergovernmental Panel on Climate Change (IPCC) appeared in March 2022 (Pörtner and Roberts, *Climate Change 2022: Impacts, Adaptation and Vulnerability*). This highly complicated and detailed report is not likely to become casual reading for the average person, but it probably should allow for an understanding and internalization of the bottom-line assessment offered by Robinson Meyer in a piece in *The Atlantic* entitled *There's no scenario in which 2050 is 'normal.'* Meyer concluded that, "We have been backed into a corner [by our inaction]. The scale of [climate] change headed our way is unimaginable. And it is also inevitable."

However, the latest IPCC report is not all "doom and gloom." The report also outlines the changes in the human way of "doing business" that have to occur to mitigate the "inevitable" effects of climate change, but these changes will have to be implemented over a distressingly short period of time. On 28 February 2022, António Guterres, the Secretary-General of the United Nations wrote that, "Nearly half of humanity is living in the danger zone—now. Many ecosystems are at the point of no return—now. Unchecked carbon pollution is forcing the world's most vulnerable on a frog march to destruction—now. The facts are undeniable. This abdication of leadership is criminal. The world's biggest polluters are guilty of arson of our only home…Today's report underscore[s] two core truths. First, coal and other fossil fuels are choking humanity. (Second,) investments in adaptation work…Delay means death" (https://media.un.org/en/asset/k1x/k1xcijxjhp; accessed 16 November 2022).

Table 21. Characteristics of the Natural Protected Areas in Guanajuato, Mexico. Abbreviations for Facilities available are as follows: A = Administrative services; R = Park guards; S = System of pathways; and V = Facilities for visitors.

Name	Category	Date of decree	Area (ha)	Municipalities	Jurisdiction	Physiographic region(s)	Area demarcated	Facilities available	Personnel present year-round	Occupied by landowners	Herpetofaunal survey completed	Management plan available
Sierra de Lobos	Sustainable use area	4 Nov 1997	127,058.0	León, San Felipe, Ocampo	State	Central Plateau	Yes	R, S, V	Yes	Yes	Partially	Yes
Cuenca Alta del Río Temascatio	Sustainable use area	29 Apr 1997	17,432.0	Salamanca, Juventino Rosas	State	Central Plateau	Yes	R, S, V	No	Yes	Partially	Yes (not updated)
Peña Alta	Sustainable use area	6 Jun 2000	13,270.2	San Diego de la Unión	State	Central Plateau	Yes	R, S	No	Yes	Partially	Yes (not updated)
Las Musas	Sustainable use area	14 May 2013	3,174.8	Manuel Doblado	State	Transmexican Volcanic Belt	Yes	R, S, V	Yes	Yes	Yes	Yes
Cerros el Culiacán y La Gavia	Sustainable use area	30 Jul 2002	32,661.5	Celaya, Cortazar, Jaral del Progreso, Salvatierra	State	Transmexican Volcanic Belt	Yes	R, S, V	Yes	Yes	Partially	Yes
Sierra de los Agustinos	Sustainable use area	17 Sep 2002	19,246.0	Tarimoro, Jerécuaro, Acámbaro	State	Transmexican Volcanic Belt	Yes	R, S, V	No	Yes	Partially	Yes (not updated)
Cerro de los Amoles	Sustainable use area	7 May 2004	6,987.0	Moroleón, Yuriria	State	Transmexican Volcanic Belt	Yes	S	No	Yes	Partially	Yes (not updated)
Cerro de Arandas	Sustainable use area	25 Nov 2005	4,816.2	Irapuato	State	Transmexican Volcanic Belt	Yes	A, S, V	No	Yes	Partially	Yes (not updated)
Presa La Purísima y su zona de influencia	Sustainable use area	26 Aug 2005	2,728.8	Guanajuato	State	Central Plateau, Transmexican Volcanic Belt	Yes	A, S, V	No	Yes	Partially	Yes (not updated)
Sierra de Pénjamo	Sustainable use area	29 May 2012	83,341.0	Cuerámaro, Manuel Doblado, Pénjamo	State	Transmexican Volcanic Belt	Yes	A, R, S, V	No	Yes	Partially	No
Cerro de Palenque	Sustainable use area	2 Nov 2012	2,030.7	Purísima del Rincón	State	Central Plateau	Yes	S	No	Yes	Partially	No
Megaparque de la Ciudad de Dolores, Hidalgo	Ecological Park	16 Dec 1997	28,44.0	Dolores Hidalgo	Stae	Central Plateau	Yes	S, V	Yes	No	Partially	Yes (not updated)
Las Fuentes	Ecological Park	26 Dec 1997	109, 03.0	Juventino Rosas	State	Transmexican Volcanic Belt	Yes	S	No	Yes	Partially	Yes (not updated)
Parque Metropolitano	Ecological Park	4 Sep 2000	337.0	León	State	Central Plateau	Yes	S, V	Yes	No	Partially	Yes (not updated)
Lago Cráter La Joya	Ecological Park	9 Apr 1999	1,479.0	Yuriria	State	Transmexican Volcanic Belt	Yes	S	No	Yes	Partially	No
Presa de Silva y áreas aledañas	Ecological Preservation Area	2 Dec 1997	8,801.0	San Francisco del Rincón, Purísima del Rincón	State	Transmexican Volcanic Belt	Yes	S	No	Yes	Partially	Yes (not updated)

Table 21 (continued). Characteristics of the Natural Protected Areas in Guanajuato, Mexico. Abbreviations for Facilities available are as follows: A = Administrative services; R = Park guards; S = System of pathways; and V = Facilities for visitors.

Name	Category	Date of decree	Area (ha)	Municipalities	Jurisdiction	Physiographic region(s)	Area demarcated	Facilities available	Personnel present year-round	Occupied by landowners	Herpetofaunal survey completed	Management plan available
Laguna de Yuriria y su zona de influencia	Ecological Preservation Area	9 Apr 1999	15.0	Yuriria	State/Federal	Transmexican Volcanic Belt	Yes	A, S, V	Yes	Yes	Partially	Yes (not updated)
Cerro del Cubilete	Ecological Preservation Area	18 Nov 2003	3,611.8	Silao, Guanajuato	State	Central Plateau, Transmexican Volcanic Belt	Yes	A, S, V	No	Yes	Partially	Yes (not updated)
Cuenca de la Soledad	Ecological Preservation Area	18 Aug 2006	2,782.0	Guanajuato	State	Central Plateau	Yes	A, S, V	No	Yes	Partially	Yes (not updated)
Presa de Neutla y su zona de influencia	Ecological Preservation Area	15 Sep 2006	2,102.4	Comonfort	State	Transmexican Volcanic Belt	Yes	S, V	No	Yes	Partially	Yes (not updated)
Región Volcánica Siete Luminarias	Natural Monument	21 Nov 1997	8,928.5	Valle de Santiago	State	Transmexican Volcanic Belt	Yes	S, V	No	Yes	Partially	Yes (not updated)
Cuenca de la Esperanza	Conservation Reserve	6 Mar 1998	1,832.7	Guanajuato	State	Central Plateau	Yes	A, R, S, V	Yes	Yes	Partially	Yes (not updated)
Pinal de Zamorano	Conservation Reserve	6 Jun 2000	13,862.0	Tierra Blanca, San José Iturbide	State	Central Plateau	Yes	S, V	No	Yes	Partially	Yes (not updated)
Sierra Gorda de Guanajuato	Biosphere Reserve	2 Feb 2007	236,882.8	Atarjea, San Luis de la Paz, Santa Catarina, Victoria, Xichú	State	Eastern Sierra Madre Oriental	Yes	A, S, V	No	Yes	Partially	No

The consideration of these dire warnings forces on us a somewhat altered viewpoint on the importance of protected areas in responding effectively to the problem of biodiversity decline. In one of the most recent entries in the Mexican Conservation Series, Cruz-Elizalde et al. (2022: 183) wrote the following: "Since humans apparently are not predisposed to deal with the threats posed to planetary biodiversity (Wilson and Lazcano 2019), i.e., to change the ways of thinking to promote the control of human population growth, conservation biologists generally propose the establishment of protected areas to ensure the safety of populations of organisms within those areas." Whereas the authors of this paper are fully in support of establishing, maintaining, and expanding the limits of such areas, under the best of circumstances this process is intended to hold at bay the encroachment of humanity on the remaining natural areas. So even if this effort is successful, these areas are cloaked by the same atmosphere that harbors the burgeoning populations of our own species. The damage to the atmosphere originating from human population centers obviously is not confined to these areas, but ultimately will impact the so-called protected areas. Again, this realization is not to be construed as an argument against setting up protected areas, but these steps alone will not guarantee protection from the ravages of humanity for an entire group of organisms, for perpetuity.

General Features of the Protected Areas in Guanajuato

Given this background, an analysis of the current level of protection offered by the areas that have been set aside in Guanajuato is presented here, beginning with the basic characteristics of these areas in Table 21. Twenty-four protected areas have been established in Guanajuato, and they fall into six categories: (1) sustainable use (11 areas); (2) ecological park (four areas); (3) ecological preservation area (five areas); (4) natural monument (one area); (5) conservation reserve (two areas); and (6) biosphere reserve (one area). These 24 areas were established from 1997 to 2013, and range in size from 15.0 to 236,882.8 ha. Most of these areas are administered at the state level, except for one at both the state and federal levels.

It is of major importance that 14 of the 24 areas are located within the Transmexican

Table 22. Distribution of herpetofaunal species in the Natural Protected Areas of Guanajuato, Mexico, based on herpetofaunal surveys. Abbreviations are as follows: * = species endemic to Mexico and ** = non-native species. The numbers of the Natural Protected Areas signify the following: 1 = Sierra de Lobos; 2 = Cuenca Alta del Río Temascatio; 3 = Peña Alta; 4 = Las Musas; 5 = Cerros el Culiacán y La Gavia; 6 = Sierra de los Agustinos; 7 = Cerro de los Amoles; 8 = Cerro de Arandas; 9 = Presa La Purísima y su zona de influencia; 10 = Sierra de Pénjamo; 11 = Cerro de Palenque; 12 = Megaparque de la Ciudad de Dolores, Hidalgo; 13 = Las Fuentes; 14 = Parque Metropolitano; 15 = Lago Cráter La Joya; 16 = Presa de Silva y áreas aledañas; 17 = Laguna de Yuriria y su zona de influencia; 18 = Cerro del Cubilete; 19 = Cuenca de la Soledad; 20 = Presa de Neutla y su zona de influencia; 21 = Región Volcánica Siete Luminarias; 22 = Cuenca de la Esperanza; 23 = Pinal de Zamorano; and 24 = Sierra Gorda de Guanajuato. Note. **Dryophytes plicata* (-) is found in the state and is part of the herpetofauna of Guanajuato, but at the moment has not been recorded in any of the natural protected areas. This species has been recorded the municipalities of Acámbaro, Salvatierra, Sa José Iturbide, and Tierra Blanca.

Taxon	Natural Protected Areas																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
AMPHIBIA (26 species)																								
Anura (23)																								
Bufonidae (5)																								
*Anaxyrus compactilis**	+	+		+	+		+	+	+	+						+		+		+				+
Anaxyrus punctatus	+	+	+		+		+	+		+			+	+						+	+		+	+
Incilius nebulifer																								+
*Incilius occidentalis**	+	+	+	+		+	+	+		+	+											+	+	+
Rhinella horribilis																								+
Craugastoridae (2)																								
Craugastor augusti		+	+	+				+		+							+	+		+				+
*Craugastor occidentalis**				+						+														
Eleutherodactylidae (3)																								
*Eleutherodactylus angustidigitorum**							+																	
Eleutherodactylus guttilatus	+	+	+	+	+								+							+				+
*Eleutherodactylus verrucipes**	+		+										+										+	+
Hylidae (5)																								
Dryophytes arenicolor				+							+		+					+	+	+	+	+	+	+
*Dryophytes eximius**	+	+	+	+	+	+	+	+	+	+	+	+					+	+	+		+	+	+	+
*Rheohyla miotympanum**																								+
Smilisca baudinii																								+
Smilisca fodiens				+																				
Microhylidae (1)																								
Hypopachus variolosus				+				+			+									+				
Ranidae (6)																								
Lithobates berlandieri	+	+	+											+									+	+
*Lithobates catesbeianus***	+													+			+							
*Lithobates megapoda**							+										+							
*Lithobates montezumae**	+	+	+		+	+	+		+								+		+				+	
*Lithobates neovolcanicus**	+	+		+	+	+	+	+	+	+	+		+		+	+	+	+		+			+	
*Lithobates spectabilis**																	+							+
Scaphiopodidae (1)																								
Spea multiplicata		+	+	+	+		+	+			+		+	+	+			+	+	+	+		+	+
Caudata (3)																								
Ambystomatidae (1)																								
*Ambystoma velasci**	+						+			+									+					+
Plethodontidae (2)																								
*Aquiloeurycea cephalica**																								+
*Isthmura bellii**						+	+															+		+
REPTILIA (71)																								
Squamata (68)																								
Lacertilia (24)																								
Anguidae (4)																								
*Abronia taeniata**																								+
*Barisia imbricata**		+	+		+		+	+			+			+	+			+	+	+	+		+	+
Gerrhonotus infernalis	+		+		+	+	+											+	+				+	

Table 22 (continued). Distribution of herpetofaunal species in the Natural Protected Areas of Guanajuato, Mexico, based on herpetofaunal surveys. Abbreviations are as follows: * = species endemic to Mexico and ** = non-native species. The numbers of the Natural Protected Areas signify the following: 1 = Sierra de Lobos; 2 = Cuenca Alta del Río Temascatio; 3 = Peña Alta; 4 = Las Musas; 5 = Cerros el Culiacán y La Gavia; 6 = Sierra de los Agustinos; 7 = Cerro de los Amoles; 8 = Cerro de Arandas; 9 = Presa La Purísima y su zona de influencia; 10 = Sierra de Pénjamo; 11 = Cerro de Palenque; 12 = Megaparque de la Ciudad de Dolores, Hidalgo; 13 = Las Fuentes; 14 = Parque Metropolitano; 15 = Lago Cráter La Joya; 16 = Presa de Silva y áreas aledañas; 17 = Laguna de Yuriria y su zona de influencia; 18 = Cerro del Cubilete; 19 = Cuenca de la Soledad; 20 = Presa de Neutla y su zona de influencia; 21 = Región Volcánica Siete Luminarias; 22 = Cuenca de la Esperanza; 23 = Pinal de Zamorano; and 24 = Sierra Gorda de Guanajuato. Note. **Dryophytes plicata* (-) is found in the state and is part of the herpetofauna of Guanajuato, but at the moment has not been recorded in any of the natural protected areas. This species has been recorded the municipalities of Acámbaro, Salvatierra, Sa José Iturbide, and Tierra Blanca.

Taxon	Natural Protected Areas																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Gerrhonotus ophiurus or *liocephalus?*																								+
Dactyloidae (2)																								
*Norops nebulosus**	+	+		+	+	+	+								+		+							
Norops sericeus																								+
Gekkonidae (1)																								
*Hemidactylus frenatus***					+																			
Phrynosomatidae (10)																								
Holbrookia maculata			+												+				+					+
*Phrynosoma orbiculare**	+	+	+										+									+	+	+
*Sceloporus aeneus**	+					+	+												+			+		
*Sceloporus dugesii**		+		+	+		+									+			+	+	+			
Sceloporus grammicus	+	+	+		+	+	+	+			+		+						+	+		+	+	+
*Sceloporus minor**	+		+								+											+	+	+
*Sceloporus scalaris**	+		+	+		+	+													+	+			+
*Sceloporus spinosus**	+	+	+	+	+			+	+	+	+		+	+	+			+	+	+			+	+
*Sceloporus torquatus**		+	+	+	+	+	+	+	+	+	+		+			+	+		+	+	+	+	+	+
Sceloporus variabilis																								+
Scincidae (3)																								
*Plestiodon dugesii**			+																					
*Plestiodon lynxe**	+		+																			+		+
Plestiodon tetragrammus																								+
Sphenomorphidae (1)																								
*Scincella selvicola**																								+
Teiidae (1)																								
Aspidoscelis gularis		+	+	+	+		+	+	+	+			+				+	+		+	+			+
Xantusiidae (2)																								
*Lepidophyma gaigeae**																								+
*Lepidophyma occulor**																								+
Serpentes (44)																								
Boidae (1)																								
Boa imperator																								+
Colubridae (18)																								
*Conopsis lineata**		+	+	+	+	+		+	+													+	+	+
*Conopisis nasus**	+	+	+		+	+	+	+		+										+		+	+	+
Drymarchon melanurus	+	+		+	+		+	+																+
*Lampropeltis mexicana**	+		+																					+
*Lampropeltis polyzona**		+		+	+	+	+	+		+	+					+	+			+	+			
*Lepthopis diplotropis**																								
Masticophis flagellum	+		+			+										+					+			+
Masticophis mentovarius	+	+		+	+	+	+	+		+	+						+			+		+	+	+
Masticophis schotti	+		+																				+	+
Oxybelis microphthalmus				+				+																+
Pantheropis emoryi																								
*Pituophis deppei**	+	+	+		+	+	+		+	+	+		+	+			+		+	+	+	+	+	+
*Pseudoficimia frontalis**	+									+														

Table 22 (continued). Distribution of herpetofaunal species in the Natural Protected Areas of Guanajuato, Mexico, based on herpetofaunal surveys. Abbreviations are as follows: * = species endemic to Mexico and ** = non-native species. The numbers of the Natural Protected Areas signify the following: 1 = Sierra de Lobos; 2 = Cuenca Alta del Río Temascatio; 3 = Peña Alta; 4 = Las Musas; 5 = Cerros el Culiacán y La Gavia; 6 = Sierra de los Agustinos; 7 = Cerro de los Amoles; 8 = Cerro de Arandas; 9 = Presa La Purísima y su zona de influencia; 10 = Sierra de Pénjamo; 11 = Cerro de Palenque; 12 = Megaparque de la Ciudad de Dolores, Hidalgo; 13 = Las Fuentes; 14 = Parque Metropolitano; 15 = Lago Cráter La Joya; 16 = Presa de Silva y áreas aledañas; 17 = Laguna de Yuriria y su zona de influencia; 18 = Cerro del Cubilete; 19 = Cuenca de la Soledad; 20 = Presa de Neutla y su zona de influencia; 21 = Región Volcánica Siete Luminarias; 22 = Cuenca de la Esperanza; 23 = Pinal de Zamorano; and 24 = Sierra Gorda de Guanajuato. Note. **Dryophytes plicata* (-) is found in the state and is part of the herpetofauna of Guanajuato, but at the moment has not been recorded in any of the natural protected areas. This species has been recorded the municipalities of Acámbaro, Salvatierra, Sa José Iturbide, and Tierra Blanca.

Taxon	Natural Protected Areas																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
*Salvadora bairdi**	+	+	+	+	+		+			+	+									+			+	+
Senticolis triaspis	+	+			+		+	+			+													+
*Tantilla bocourti**	+	+	+		+				+										+	+			+	
Tantilla rubra																								+
Trimorphodon tau		+	+	+	+	+	+	+	+	+									+	+	+		+	+
Dipsadidae (10)																								
Diadophis punctatus	+		+	+	+		+							+					+	+				
*Geophis dugesii**					+	+	+																	
*Geophis latifrontalis**																								+
*Geophis petersii**							+																	
Hypsiglena jani	+	+			+						+												+	+
*Hypsiglena tanzeri**																								+
Leptodeira septentrionalis																							+	+
*Rhadinaea gaigeae**																								+
*Rhadinaea hesperia**	+					+	+		+	+														
*Rhadinaea teaniata**																								+
Elapidae (1)																								
Micrurus tener		+	+	+	+		+	+					+				+		+				+	+
Natricidae (8)																								
Storeria dekayi																								+
*Storeria storerioides**	+	+	+		+	+												+				+	+	+
Thamnophis cyrtopisis	+	+	+	+		+	+				+									+				+
Thamnophis eques	+	+	+		+	+		+	+	+					+								+	+
*Thamnophis melanogaster**		+			+		+		+								+			+				
*Thamnophis pulchrilatus**																								+
*Thamnophis scalaris**	+						+															+		+
*Thamnophis scaliger**	+				+	+																		
Typhlopidae (1)																								
*Virgotyphlops braminus***	+	+		+				+											+					
Viperidae (5)																								
*Crotalus aquilus**	+	+	+		+	+	+	+			+								+			+	+	+
Crotalus atrox																								+
Crotalus molossus	+	+	+	+	+	+		+		+	+		+	+	+		+	+	+	+		+	+	+
*Crotalus polystictus**	+						+		+	+	+													
Crotalus scutulatus	+		+																					+
Testudines (3)																								
Kinosternidae (2)																								
Kinosternon hirtipes	+	+	+	+			+		+	+			+			+			+		+			
*Kinosternon integrum**	+	+	+	+	+		+	+	+	+	+		+			+			+	+		+	+	+
Emydidae (1)																								
*Trachemys scripta***																								+

Table 23. Summary of the distributional status of the herpetofaunal species in the protected areas in Guanajuato, Mexico. Total = total number of species recorded in all of the listed protected areas.

Protected area	Number of species	Distributional status		
		Non-endemic (NE)	Country Endemic (CE)	Non-native (NN)
Sierra de Lobos	47	17	28	2
Cuenca Alta del Río Temascatio	39	17	21	1
Peña Alta	40	19	21	—
Las Musas	31	16	14	1
Cerros el Culiacán y La Gavia	37	15	21	1
Sierra de los Agustinos	26	8	18	—
Cerro de los Amoles	40	13	27	—
Cerro de Arandas	27	14	12	1
Presa La Purísima y su zona de influencia	17	4	13	—
Sierra de Pénjamo	24	8	16	—
Cerro de Palenque	22	9	13	—
Megaparque de la Ciudad de Dolores, Hidalgo	1	—	1	—
Las Fuentes	16	9	7	—
Parque Metropolitano	9	5	3	1
Lago Cráter La Joya	8	4	4	—
Presa de Silva y áreas aledañas	8	2	6	—
Laguna de Yuriria y su zona de influencia	16	5	10	1
Cerro del Cubilete	12	6	6	—
Cuenca de la Soledad	23	10	12	1
Presa de Neutla y su zona de influencia	27	13	14	—
Región Volcánica Siete Luminarias	14	7	7	—
Cuenca de la Esperanza	19	4	15	—
Pinal de Zamorano	32	14	18	—
Sierra Gorda de Guanajuato	69	34	34	1
Total	97	38	55	4

Volcanic Belt, the physiographic region of greatest importance in Guanajuato, since the TVB contains a herpetofauna almost equivalent to that of the Sierra Madre Oriental, the largest number of country endemic species, and the greatest number of high vulnerability species.

In all 24 cases, the areas are demarcated. Only two of the 24 areas encompass the full range of services; while almost one-half of the areas provide either park guards, a system of pathways, and facilities for visitors (five areas) or administrative services, a system of pathways, and facilities for visitors (six areas). Unfortunately, personnel are present year-round in only seven of the 24 areas. Similarly, only two of the 24 areas are not occupied to some degree by private landowners.

Most herpetofaunal surveys in the protected areas only have been partially completed, and although management plans are available for most areas, they have not been updated. Currently, plans are available for 20 areas, but not for the other four areas.

Effectiveness of the Protected Areas in Guanajuato

In order to determine the effectiveness of the 24 protected areas in Guanajuato, the available herpetofaunal records have been assembled for each of these areas and the results are shown in Table 22, and summarized in Table 23.

Of the 101 species documented for the herpetofauna of Guanajuato, 97 (96.0%) have been recorded in the 24 protected areas in the state (Table 23). Thus, all but four species have been recorded for the compendium of the 24 protected areas. This favorable situation is far better than has been reported in some other Mexican Conservation Series entries.

The four species recorded for the state that have not been reported from one or more of the protected areas are: the hylid frog *Dryophytes plicatus*, the gekkonid lizard *Hemidactylus turcicus*, the dipsadid snake *Geophis sartorii*, and the natricid snake *Adelophis copei*. Fortunately, three of these four species are native to Guanajuato, while *H. turcicus* is a non-native species and thus not desirable within the natural protected areas.

The numbers of protected areas (of a total of 24) inhabited by the 97 species range from one to 19. The sizes of the herpetofaunas of these 24 areas range from one for the Megaparque de la Ciudad de Dolores, Hidalgo to 69 for the Sierra Gorda de Guanajuato (mean, 24.8). However, additional work is necessary to fully document the herpetofauna of these natural protected areas.

In most cases, the number of country endemic species in each area exceeds that of the non-endemic species (16 of 24 areas, or 66.7%). In the other eight cases, either the

numbers of these groups of species are the same (four of 24 areas, or 16.7%) or the number of non-endemic species is higher than the number of country endemic species (four of 24 areas, or 16.7%).

All 40 of the non-endemic species and 53 of the 56 country endemic species (94.6%) have been recorded in the compendium of the 24 protected areas. Although their presence in the protected areas is not desirable, four-fifths (9 species, or 80.0%) of the non-native species have been recorded in one or more of the 24 areas. The most widely distributed non-native species is *Virgotyphlops braminus*, which has been reported in five of the 24 areas. Not surprisingly, this fossorial snake is one of the two most widely distributed non-native species in Mexico (Cruz-Elizalde et al. 2022). What is surprising is that the other non-native species, *Hemidactylus frenatus* (Cruz-Elizalde et al. 2022), has been reported from only one of the 24 areas.

Conclusions and Recommendations

Conclusions

A. Presently, the herpetofauna of Guanajuato consists of 101 species, including 24 anurans, three salamanders, 71 squamates (25 lizards and 46 snakes), and three turtles.

B. The numbers of herpetofaunal species recorded from the three physiographic regions in Guanajuato range from 60 in the Central Plateau to 75 in the Sierra Madre Oriental.

C. The numbers of species shared among the physiographic regions range from 44 between the Central Plateau and the Sierra Madre Oriental to 56 between the Central Plateau and the Transmexican Volcanic Belt. The Coefficient of Biogeographic Resemblance values range from a low of 0.65 between the Central Plateau and the Sierra Madre Oriental to 0.84 between the Central Plateau and the Transmexican Volcanic Belt. The UPGMA dendrogram demonstrates that the Central Plateau (CP) and the Transmexican Volcanic Belt (TVB) cluster with one another at the 0.84 level and that the Sierra Madre Oriental (SM) region clusters with the other two regions at the 0.65 level. This clustering pattern is consistent with the fact that the CP and TVB regions are similarly large in size within the state (Fig. 10) and are located adjacent to one another, and that the SMO is the smallest region in the state and is adjacent only to the CP region.

D. The level of endemism in the Guanajuato herpetofauna is relatively high. Of the 101 species comprising the entire state herpetofauna, 56 (55.4%) are country endemics including 12 anurans (50.0% of 24 species), three salamanders (100% of three species), 15 lizards (60.0% of 25 species), 25 snakes (54.3% of 46 species), and one turtle (33.3% of three turtles). Thirty-nine percent of the state endemics in Guanajuato are squamates of the genera *Abronia* (one species), *Barisia* (one), *Norops* (one), *Phrynosoma* (one), *Sceloporus* (six), *Plestiodon* (two), *Scincella* (one), *Lepidophyma* (two), *Conopsis* (two), *Lampropeltis* (two), *Leptophis* (one), *Pituophis* (one), *Pseudoficimia* (one), *Salvadora* (one), *Tantilla* (one), *Geophis* (three), *Hypsiglena* (one), *Rhadinaea* (three), *Adelophis* (one), *Storeria* (one), *Thamnophis* (four), and *Crotalus* (two).

E. The distributional status of the 101 members of the Guanajuato herpetofauna is as follows (in order of decreasing species numbers): country endemics (56, 55.4%); non-endemics (40, 39.6%); and non-natives (5, 5.0%).

F. The 40 non-endemic species are placed in the following distributional categories: MXUS (26, 65.0%); USCA (six, 15.0%); MXCA (four, 10.0%); MXSA (three, 7.5%); and USSA (one, 2.5%).

G. The principal environmental threats to the herpetofauna of Guanajuato are agriculture, industry, forestry, cattle production, and mining.

H. The conservation status of the herpetofauna of Guanajuato was assessed using the SEMARNAT, IUCN, and EVS systems. As with all previous MCS studies, the SEMARNAT system was found to be of minimal utility, inasmuch as only 44 of 96 species have been evaluated using this system. Of these 44 species, 16 are allocated to the Threatened (A) category and 28 to the Special Protection (Pr) category. The use of the SEMARNAT system does not appear to be biased toward evaluating endemic species as opposed to non-endemic species; although it has not been applied to a sufficient segment of the Guanajuato herpetofauna to be of much use.

I. Application of the IUCN conservation system by category and the proportions of the 96 native species in Guanajuato are as follows: EN (one species, 1.0%); VU (nine, 9.4%); NT (three, 3.1%); LC (71, 74.0%); DD (five, 5.2%); and NE (seven, 7.3%).

J. Application of the EVS system of conservation assessment to the 96 native Guanajuato species indicates that the categorical values increase from low scores (31 species, 32.3%) to medium scores (41 species, 42.7%), and then decreases to high scores (24 species, 25.0%).

K. A comparison of the IUCN and EVS conservation status categorizations indicates that 41.7% of the 24 high vulnerability species (by EVS) are allocated to one of the two IUCN "threat categories" (EN or VU), and that 83.9% of the 31 low vulnerability species are placed in the LC category. As in all previous MCS studies, the correlation between the results of applying the IUCN and EVS systems is relatively poor.

L. An examination of the 83 native species (86.5% of all 96) placed into the IUCN DD, NE, and LC categories demonstrates that many of these species have been evaluated improperly when compared to their

respective EVS values, so we indicated how these species might be reassessed in the IUCN system to better reflect their prospects for survival in perpetuity.

M. The RHP measure was utilized to ascertain the conservation significance of the three regional herpetofaunas in Guanajuato. This analysis demonstrates that the most significant regional herpetofauna is that of the Transmexican Volcanic Belt, as it contains a herpetofauna only slightly smaller than that of the Sierra Madre Oriental, the largest number of country endemic species (43, 76.8% of 56 species), and the greatest number of high vulnerability species (18, 26.1% of 69 species).

N. Twenty-four protected areas are established in Guanajuato, most at the state level. Fourteen of these areas are in the Transmexican Volcanic Belt, two of which overlap onto the Central Plateau, and the Transmexican Volcanic Belt is the most important herpetofaunal region in the state. Unfortunately, landowners occupy most areas, most herpetofaunal surveys have only been partially completed, and management plans are generally available but seldom updated.

O. Collectively, the unusually high number of protected areas are shown to harbor 97.0% of the species recorded for the state of Guanajuato, which is a highly desirable situation. Even so, much work remains to be done to fully document the herpetofauna in these protected areas.

P. The 97 species recorded in the state's protected areas includes all 38 of the non-endemic species and 55 of the 56 country endemic species. In addition, although not desirable in these areas, four of the five non-native species also have been recorded. The most widely distributed of these non-native species is *Virgotyphlops braminus*.

Recommendations

A. This survey demonstrated that 97 of the 101 species that comprise the herpetofauna of Guanajuato have been recorded in the 24 protected areas established in the state thus far. This is a highly desirable state of affairs, and can be used as a starting point in securing a future for the herpetofauna of this rather highly urbanized state.

B. Evidently, however, the degree of completeness of the herpetofaunal surveys varies from one protected area to another. Thus, our most basic recommendation is to provide additional studies in each of these areas, especially those that are now the least studied.

C. Once reasonably complete herpetofaunal surveys are available for each of the 24 natural protected areas, monitoring programs can be established to continually assess the health of populations of the constituent species. Additionally, efforts should be made to determine whether the two native species (*Dryophytes plicatus* and *Adelophis copei*) that have not been recorded from any of the 24 areas can be found, so they can be included in ongoing monitoring programs.

D. These steps should be taken with urgency, given that the small state Guanajuato is the 6th most populous and the 5th most densely populated in the country.

"How to serve both humanity and the rest of life is the great challenge of the modern era."

Edward O. Wilson (2014)

Acknowledgments.—We are thankful to the following people for providing some of the images used in this paper: José Carlos Arenas-Monroy; Samuel Cadena-Rico: Yadira Fabiola Estrada-Sillas; María del Carmen Mendoza-Portilla; and Mará Fernanda Rodríguez-Gutiérrez.

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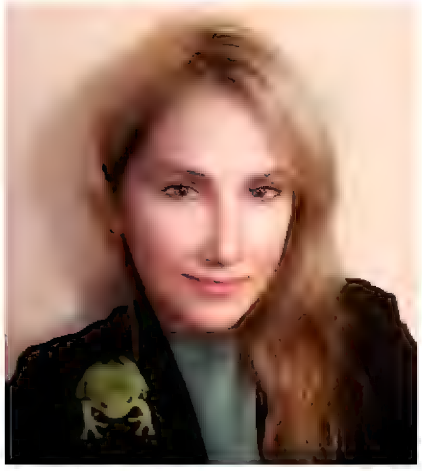
Óscar Báez-Montes received his B.S. and M.S. degrees from the Universidad de Guadalajara in Mexico. His interests include the ecology and conservation of terrestrial vertebrates and their relationships to human communities. Óscar has worked with diverse groups of fauna in areas of conservation importance, such as priority terrestrial regions, Ramsar sites, and natural protected areas in the Mexican Plateau and Western Mexico. He is currently a part-time professor at the Universidad Autónoma de Guadalajara in Mexico. He has three children, Ian, Max, and Regina, and a loving wife Faby (also a Biologist) who accompanies him during his fieldwork.

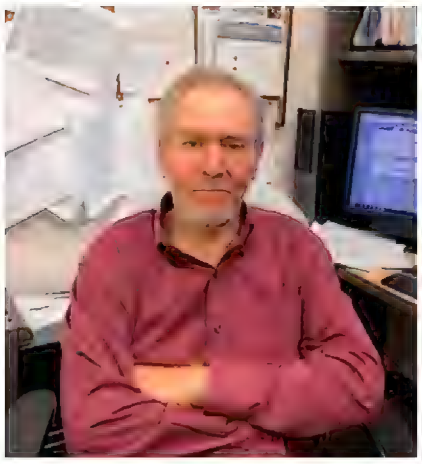


Lydia Allison Fucsko, who resides in Melbourne, Australia, is an environmental activist and amphibian conservationist. As a photographer with international publications, she has taken countless amphibian photographs, including photo galleries of frogs mostly from southeastern Australia. Lydia has a Bachelor of Humanities from La Trobe University (Bundoora, Victoria, Australia), a Diploma in Education from the University of Melbourne (Parkville, Victoria, Australia), and postgraduate diplomas in computer education and in vocational education and training from the University of Melbourne (Parkville). Additionally, Lydia has a Master's degree in Counseling from Monash University (Clayton, Victoria, Australia). She received her Ph.D. in Environmental Education, which promoted habitat conservation, species perpetuation, and global sustainable management, from Swinburne University of Technology (Hawthorn, Victoria, Australia), while being mentored by the late Australian herpetologist and scholar Michael James Tyler (Order of Australia recipient). As a sought-after educational consultant, Lydia has academic interests that include: clinical psychology, focusing on psychopathology; neuroscience and empathy; environmental education for sustainable development; sentient ecology; academic writing; and creative writing, which includes poetry and creative non-fiction books for children and young adults. Lydia is the senior author (with Boria Sax) of a chapter in the 2019 *Springer Encyclopedia of Sustainability in Higher Education* entitled "Learning activities for environmental education for sustainable development." Recently, she has co-authored an obituary of Jaime D. Villa, a study of the introduced Mesoamerican herpetofauna, a treatment of the conservation prospects of the Mesoamerican salamander fauna, papers on the herpetofauna of Veracruz and Querétaro, Mexico, a review of the books *Advances in Coralsnake Biology* and *Lizards of Mexico, Part 1*, and a study on the biological and cultural diversity of Oaxaca, Mexico, among several other academic papers. In 2020, the species *Tantilla lydia*, with the suggested common name of Lydia's Little Snake, was named in her honor.

Dominic L. DeSantis is an Assistant Professor of Biology at Georgia College and State University, Milledgeville, Georgia, USA, in the Department of Biological and Environmental Sciences. Dominic's research interests broadly include the behavioral ecology, conservation biology, and natural history of herpetofauna. In addition to ongoing collaborative projects associated with the Mesoamerican Research Group, much of Dominic's current research focuses on using novel animal-borne sensor technologies to study the behavior of snakes in the field. While completing his Ph.D. at the University of Texas at El Paso, Dominic accompanied Vicente Mata-Silva, Elí García-Padilla, and Larry David Wilson on survey and collecting expeditions to Oaxaca in 2015, 2016, and 2017, and is a co-author on numerous natural history publications produced from those visits, including an invited book chapter on the conservation outlook for herpetofauna in the Sierra Madre del Sur of Oaxaca.

Elí García-Padilla is a Social Biologist and Professional Photographer with more than 12 years of experience in the formal study and photo documentation of the biological and cultural diversity of Mexico. He has published one book, entitled *Mexican Biodiversity: the Snake, the Jaguar and the Quetzal*, and more than 100 formal contributions on knowledge, the communication of science and the conservation of Mesoamerican biodiversity. Since 2006, Elí has been exploring Oaxaca and Chiapas, which are the most biodiverse and multicultural states in Mexico. In 2017, he began to enter the mythical region of Los Chimalapas in the Isthmus of Tehuantepec, which is the most biologically rich region in all of Mexico, under a community social conservation scheme. Elí has published his photographic work in prestigious magazines such as *National Geographic* in Spanish and *Cuartoscuro*. In 2020, he co-founded the Mesoamerican Biodiversity initiative with the aim of creating a community around the dissemination of the most important wealth of Mexico, which is its biodiversity and its culture. His writings are published regularly in *Oaxaca Media*, the *Jornada Ecológica* and the *Ojarasca Supplement* of *La Jornada*.

Arturo Rocha is a Ph.D. student in the Ecology and Evolutionary Biology program at the University of Texas at El Paso. His interests include the study of the biogeography, physiology, and ecology of amphibians and reptiles in the southwestern United States and Mexico. A graduate of the University of Texas at El Paso, his thesis centered on the spatial ecology of the Trans-Pecos Rat Snake (*Bogertophis subocularis*) in the northern Chihuahuan Desert. To date, he has authored or co-authored over 20 peer-reviewed scientific publications.



Jerry D. Johnson is Professor of Biological Sciences at The University of Texas at El Paso, and has extensive experience studying the herpetofauna of Mesoamerica, especially southern Mexico. Jerry is the Director of the 40,000-acre Indio Mountains Research Station, was a co-editor on *Conservation of Mesoamerican Amphibians and Reptiles* and co-author of four of its chapters. He is also the senior author of the recent paper "A conservation reassessment of the Central American herpetofauna based on the EVS measure" and is the Mesoamerica/Caribbean editor for the Geographic Distribution section of *Herpetological Review.* Jerry has authored or co-authored over 142 peer-reviewed papers, including two 2010 articles, "Geographic distribution and conservation of the herpetofauna of southeastern Mexico" and "Distributional patterns of the herpetofauna of Mesoamerica, a Biodiversity Hotspot." One species, *Tantilla johnsoni*, has been named in his honor. Presently, Jerry is Co-chair of the Taxonomic Board for the journal *Mesoamerican Herpetology*.

Louis W. Porras graduated with a degree in Biology in 1971 from what today is known as Miami-Dade College in Florida, USA. Over his career, he has authored or co-authored over 60 academic publications, including the descriptions of two new species, and two taxa have been named in his honor. Louis developed an interest in herpetology at an early age in his native Costa Rica. His passion for the field led him to travel to many remote areas, including sites throughout the Bahamas, the United States, Mesoamerica, and parts of South America. In 1968, he worked at the Houston Zoological Gardens, and from 1982 to 1984 at Utah's Hogle Zoo. In 1976, he attended the inaugural meeting of the International Herpetological Symposium (IHS), and later served the group as Vice-President and President. In 1993, along with Gordon W. Schuett, he helped launch the journal *Herpetological Natural History*, and for the 20th anniversary of IHS, in recognition of his contributions, three former Presidents dedicated the book *Advances in Herpetoculture* in his honor. Louis' career in publishing began in 1995, when he helped publish *Fauna* magazine as a member of Canyonlands Publishing Group. In 2002, he founded Eagle Mountain Publishing, LC, which has published such herpetological titles as *Biology of the Vipers* (2002), *Biology of the Boas and Pythons* (2007), *Amphibians, Reptiles, and Turtles in Kansas* (2010), *Conservation of Mesoamerican Amphibians and Reptiles* (2010), and *Amphibians and Reptiles of San Luis Potosí* (2013). From 2014 to 2018 Louis was the Publisher and Managing Editor of the journal *Mesoamerican Herpetology*, and recently he was the Publisher and Co-editor of the book *Advances in Coralsnake Biology: with an Emphasis on South America*.

Larry David Wilson is a herpetologist with lengthy experience in Mesoamerica. He was born in Taylorville, Illinois, USA, and received his university education at the University of Illinois at Champaign-Urbana (B.S. degree) and at Louisiana State University in Baton Rouge (M.S. and Ph.D. degrees). He has authored or co-authored more than 470 peer-reviewed papers and books on herpetology. Larry is the senior editor of *Conservation of Mesoamerican Amphibians and Reptiles* (2010) and the co-author of seven of its chapters. His other books include *The Snakes of Honduras* (1985), *Middle American Herpetology* (1988), *The Amphibians of Honduras* (2002), *Amphibians & Reptiles of the Bay Islands and Cayos Cochinos, Honduras* (2005), *The Amphibians and Reptiles of the Honduran Mosquitia* (2006), and *Guide to the Amphibians & Reptiles of Cusuco National Park, Honduras* (2008). He is also the co-author of 14 previous entries in the Mexican Conservation Series dealing with the herpetofauna of the states of Michoacán, Oaxaca, Chiapas, Tamaulipas, Nayarit, Nuevo León, Jalisco, Puebla, Coahuila, Hidalgo, Veracruz, Querétaro, and Tabasco, as well as the tri-state Mexican Yucatan Peninsula. In addition, he is a co-author of several significant publications on the development and extensive application of the EVS measure and on conservation issues related to the Mexican herpetofauna at the national level. To date, he has authored or co-authored the descriptions of 76 currently-recognized herpetofaunal species, and seven species have been named in his honor, including the anuran *Craugastor lauraster*, the lizard *Norops wilsoni*, and the snakes *Oxybelis wilsoni*, *Myriopholis wilsoni*, and *Cerrophidion wilsoni*, as well as the oligochaete annelid *Pheretima wilsoni*, and the coccidian parasite *Caryospora wilsoni*. In 2005, he was designated a Distinguished Scholar in the Field of Herpetology at the Kendall Campus of Miami-Dade College by the then-campus president Dr. Wasim Shomar. Currently, Larry is a Co-chair of the Taxonomic Board for the website *Mesoamerican Herpetology*.

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16(2) [General Section]: 181–214 (e322).

Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi River drainages. Part 2: Lizards (Sauria), chelonians, and crocodiles

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***Abstract.*—This work is the second report of the results obtained from a series of rapid biodiversity surveys of the upper Cuito, Cubango, Cuando, Zambezi, and Kwanza River basins in Angola, which were conducted between 2015 and 2019 in conjunction with the National Geographic Okavango Wilderness Project. The herpetofauna of this region are poorly documented and the results of these surveys help to address the knowledge gap regarding the conservation importance of this region. Here, an updated checklist is provided for the current and historical records of lizards, chelonians, and crocodiles from the southeastern region of Angola. A total of 369 new records were documented comprising 40 species, bringing the total number of recognized lizard, chelonian, and crocodile species in this region to 58. These surveys documented four new country records (i.e., *Lygodactylus chobiensis*, *Agama armata*, *Pachydactylus wahlbergii*, and *Ichnotropis* cf. *grandiceps*) and increased the total number of reptile species known to occur in Angola (excluding snakes) from approximately 157 to 161. Finally, updated distribution maps for the whole country are provided for all of the species encountered in this study.**

Key words. Africa, Cuanavale, Cuito, headwaters, Okavango Delta, reptile

***Resumo.*—Este trabalho é a segunda parte dos resultados de uma série de levantamentos rápidos de biodiversidade realizados nas bacias dos rios Cuito, Cubango, Cuando, Zambeze e Kwanza em Angola, entre 2015 e 2019, em conjunto com o National Geographic Okavango Wilderness Project. A herpetofauna desta região está pouco documentada, e os resultados destes levantamentos ajudarão a colmatar a lacuna de conhecimento sobre a importância da sua conservação. Aqui apresentamos uma lista atualizada de registos históricos e recentes dos lagartos, quelónios e crocodilos do sudeste de Angola. Ao todo, foram documentado 369 novos registros, relativos a 40 espécies, elevando o número total de espécies desses três grupos na região para 58. Nestes levantamentos foram registadas em Angola pela primeira vez quatro as espécies de lagartos (*Lygodactylus chobiensis*, *Agama armata*, *Pachydactylus wahlbergii*, *Ichnotropis* cf. *grandiceps*), aumentando o número total de espécies conhecidas de répteis (excluindo cobras) de Angola de 157 para 161. Por fim, apresentamos mapas de ocorrência/distribuição atualizados das espécies encontradas neste estudo para todo o país.**

Palavras-chave. África, Cuanavale, Cuito, Delta do Okavango, nascentes, réptil

Citation: Conradie W, Keates C, Verburgt L, Baptista NL, Harvey J, Júlio T, Neef G. 2022. Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi River drainages. Part 2: Lizards (Sauria), chelonians, and crocodiles. *Amphibian & Reptile Conservation* 16(2) [General Section]: 181–214 (e322).

Accepted: 18 November 2022; **Published:** 8 December 2022

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Introduction

A surge of studies on the Angolan herpetofauna has occurred in the last decade, including numerous new species descriptions. This is especially true for lizards (Order Sauria), with 28 species newly described during this period (Conradie et al. 2012, 2022; Stanley et al. 2016; Branch et al. 2019a, 2021; Marques et al. 2019a,b, 2020, 2022a,b; Ceríaco et al. 2020a,b,c; Lobón-Rovira et al. 2021, 2022a; Parrinha et al. 2021; Wagner et al. 2021), and many more descriptions in preparation (e.g., Bates et al., pers. comm.). In addition, the taxonomic revisions in those studies have further refined the number of lizard species occurring in Angola, and they are the result of numerous collaborative biodiversity surveys which have also added many new country records (Marques et al. 2020; Lobón-Rovira et al. 2022b).

The most recent synthesis of Angolan reptiles, excluding snakes (Conradie et al. 2021), set the national total at 145 species (Marques et al. 2018; Branch et al. 2019b). Considering the new additions mentioned above and the results of taxonomic revisions since 2018, this elevates the total number of recognized species of lizards, chelonians, and crocodiles for Angola to 157 (excluding cases of unconfirmed subspecies status). The currently known Angolan lizard richness is nearly half that of South Africa (157 versus 286 species), a country almost equivalent in size and biome diversity (Branch et al. 2019b). This is higher than in neighboring countries to the east and north (Botswana ~74, Democratic Republic of the Congo [DRC] ~105, and Zambia ~81), and slightly lower than countries to the south (Namibia ~178) (Pietersen et al. 2021; Uetz et al. 2022; W. Conradie, unpub. data).

Branch et al. (2019b) predicted that at least 75 new lizard species will be added to the growing national list, and if the current rate of ~4 species per year is maintained, this estimate will be exceeded in less than two decades. This will make Angola one of the most herpetofauna-rich countries in mainland Africa.

This paper is the second installment in a series of articles which document the herpetofauna of the poorly studied southeastern Angolan region. The first provided a synthesis of the snakes of this region (Conradie et al. 2021), while the present paper focuses on lizards, chelonians and crocodiles, and a third paper on the amphibians is in preparation. The overarching aim of this project is to document and quantify the herpetofaunal diversity and richness of southeastern Angola, and improve our knowledge of the conservation importance of this area in both regional and national contexts.

Methods

See Conradie et al. (2021) for details on the number of surveys conducted, as well as a description of the study area, sampling techniques, and species mapping procedure. The specific methods pertaining to this paper are provided here.

Species Identification and Morphology

Upon completion of the fieldwork component of this study, preliminary species identifications were made using relevant field guides or published identification keys (FitzSimons 1943; Branch 1998; Pietersen et al. 2021) and through comparisons with material housed in the Port Elizabeth Museum (PEM). Nomenclature was based on the online Reptile Database (Uetz et al. 2022) and was updated as needed. Common names follow Marques et al. (2018) and Pietersen et al. (2021).

Snout-vent length (SVL, measured from the tip of the snout to the posterior end of the cloacal scale or vent opening) and tail length (TL, measured from the cloacal opening to the tip of the tail) were measured to the nearest 0.1 mm using a digital calliper. For the sake of brevity, in presenting these measurements, the SVL is presented first, followed by an addition sign (+) and then the TL is given. The following basic scale counts were also documented using a Nikon SMZ1270 binocular stereo microscope: number of scale rows at midbody; number of transverse scale rows dorsally (along the vertebral line, from the nuchal [excluded from count] to base of the tail; except for Lacertidae and Agamidae, where this was counted from the shoulder to the base of the tail); number of transverse scale rows ventrally (along the midline, from the mental [excluded from count] to the cloacal plate [excluded]; except for Lacertidae and Agamidae, where they were counted from the shoulder to the groin); number of longitudinal rows of ventral scales or enlarged ventral plates in Lacertidae and Gerrhosauridae; number of subdigital lamellae under 4th toe; number of supraciliaries; number of supralabials (in Lacertidae, but in Scincidae only those anterior to the subocular were counted); number of infralabials; number of femoral or precloacal pores (including number of rows, as observed in agamids); and maximum number of keels per scale. Where scale or pore counts are presented from both sides of the body they are separated by a slash (/) with the right counts given first, then the left counts. For amphisbaenids, the following additional scale counts were recorded: number of body annuli (counted dorsally from behind the head shields to anterior to the precloacal shield) and number of caudal annuli (counted ventrally from the posterior cloacal cap to the last annulus). Each scale count is presented as a range with the average in parentheses.

Results

The surveys yielded a total of 283 individual lizard, 12 chelonian, and 74 crocodile records from approximately 321 unique localities in southeastern Angola, primarily around the source lakes of the Cuito, Cuanavale, Cuando

and Quembo rivers. Herpetofauna trap arrays (see Conradie et al. 2021) were deployed for a total of 240 trap nights and resulted in the capture of 68 specimens comprising 12 species (Table 1). A total of 30 lizard species (comprising eight families and 17 genera), four chelonians (two families and two genera), and one crocodile were recorded during this study (Table 2). Five additional species (*Acanthocercus margaritae*, *Afroedura wulfhaackei*, *Ichnotropis bivitatta*, *Hemidactylus mabouia*, and *Trachylepis sulcata ansorgii*) are reported here. Although they were not collected from the defined core study area, these species are expected to occur within this area. Updated Angolan species distribution maps are provided for each of the 40 species discussed in this paper (Maps 1–40). The mapping exercise included collating 1,665 unique records: 626 historical records from Marques et al. (2018), 261 additional literature records, 171 virtual museum records, and 507 additional records mostly from our surveys or unpublished records in the Port Elizabeth Museum and Ditsong National Museum of Natural History (formerly Transvaal Museum, TM) collections. This mapping exercise increased the number of Angolan records for the 40 species of lizards, chelonians, and crocodiles by 65.6%.

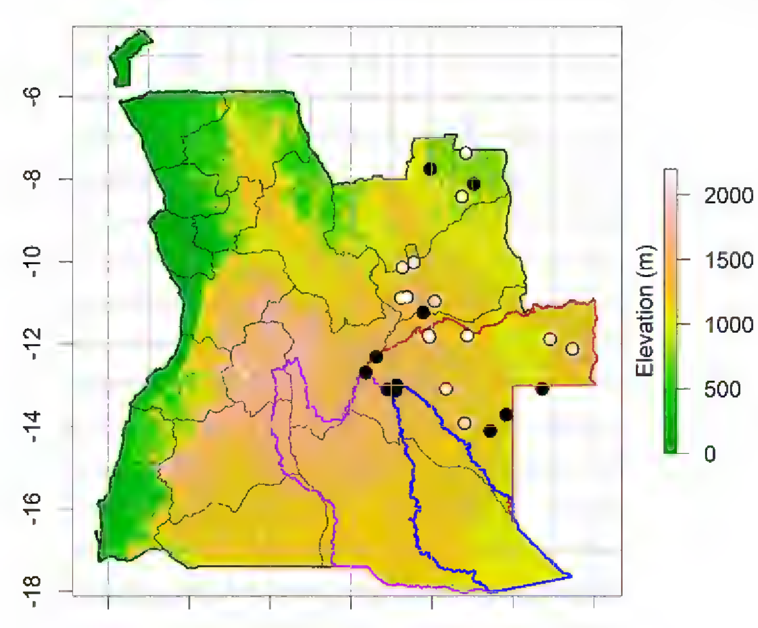
Fig. 1. Adult female *Acanthocercus* cf. *cyanocephalus* (PEM R23560) from Quembo River source. *Photo by Werner Conradie.*

Fig. 2. Adult male *Acanthocercus* cf. *cyanocephalus* (PEM R27387) from Luvu River camp. *Photo by Chad Keates.*

What follows is a checklist of all lizard, chelonian, and crocodile species found during these surveys. The account for each species includes a list of material examined, brief descriptions of newly collected material, and comments on habitat/natural history and taxonomy. Detailed morphological data and natural history notes, mostly for the adult material, can be found in Supplementary Table 1 at: https://doi.org/10.6084/m9.figshare.21670706.v1. The new distributional data used to compile the distribution maps can be found in Supplementary Table 2 at: https://doi.org/10.6084/m9.figshare.21670676. Abbreviations: asl, above sea level; DOR, dead on road; 't' after measurements refers to truncated, and 'r' refers to regenerated.

Reptilia
Squamata
Sauria
Agamidae

Acanthocercus cf. *cyanocephalus* (Falk, 1925)
Angolan or Western Tree Agama (Figs. 1–2, Map 1)
Material (9 specimens): PEM R23267, Cuanavale River source, -13.09330° 18.89396°, 1,367 m asl; PEM R23318, Cuito River source, -12.68935° 18.36012°, 1,435 m asl; PEM R23480, Cuando River source, -13.00164° 19.12960°, 1,372 m asl; PEM R23503, Sombanana village, -12.31082° 18.62392°, 1,403 m asl; PEM R23517, near Cuito River source, -12.68563° 18.36686°, 1,460 m asl; PEM R23529, INBAC: WC-4588, drive back from Quembo River source, -13.10543° 19.01698°, 1,555 m asl; PEM R23560, old hunters camp near Quembo River source, -13.13167° 19.09639°, 1,290 m asl; PEM R27387, Luvu River camp, -13.71200° 21.83538°, 1,082 m asl. **Description:** The absence of an enlarged occipital scale and its arboreal habits allow the distinction between sympatric congeners and *Agama*



Map 1. Distribution of *Acanthocercus* cf. *cyanocephalus* in Angola. Historical records are indicated by white dots while all new records are indicated by black dots. Axis values are in degrees (°). Purple polygon – Okavango River basin, blue polygon – Cuando River basin, brown polygon – Zambezi River basin.

Table 1. Herpetofauna drift fence funnel trap array sites for the 2016–2019 surveys, with coordinates presented in the WGS84 datum, elevation, brief habitat description, number of days installed (expressed as "trap nights"), and number of captures. R = river.

Trap site	Latitude	Longitude	Elevation (m asl)	Habitat description	Dates	Trap nights	Captures
Cuito R. 1	-12.688693	18.360164	1,426	Marginal vegetation at source lake	15–25 Feb 2016	10	9
Cuito R. 2	-12.688956	18.361870	1,438	Miombo woodland	15–25 Feb 2016	10	4
Cuito R. 3	-12.686020	18.364500	1,414	Grassy south-facing slope with scattered shrubs	16–25 Feb 2016	9	0
Cuanavale R. 1	-13.088937	18.892570	1,360	Marginal grassy vegetation at source lake	27 Feb–15 Mar 2016	18	2
Cuanavale R. 2	-13.092677	18.895518	1,357	Marginal grassy vegetation at source lake	27 Feb–15 Mar 2016	18	0
Cuanavale R. 3	-13.092813	18.894921	1,361	Degraded/secondary miombo woodland and grass	28 Feb–15 Mar 2016	17	2
Cuanavale R. 4	-13.050780	18.897450	1,396	Sandy basin with scattered grass	30 Feb–15 Mar 2016	15	6
Quembo R. 1	-13.135917	19.044167	1,369	Marginal grassy vegetation at source lake	27 Oct–11 Nov 2016	13	4
Quembo R. 2	-13.135444	19.043972	1,375	Miombo woodland	27 Oct–11 Nov 2016	13	2
Quembo R. 3	-13.130725	19.037245	1,443	Miombo woodland	29 Oct–11 Nov 2016	12	1
Quembo R. 4	-13.135863	19.047088	1,368	Marginal grassy vegetation at source lake	27 Oct–11 Nov 2016	12	6
Cuando R. 1	-13.003929	19.128079	1,351	Marginal grassy vegetation at source lake	12–23 Nov 2016	11	1
Cuando R. 2	-13.004259	19.127187	1,350	Marginal grassy vegetation at source lake	12–23 Nov 2016	11	0
Cuando R. 3	-13.003337	19.135640	1,360	Grassland	13–23 Nov 2016	10	1
Cuando R. 4	-13.001637	19.129598	1,374	Degraded/secondary miombo woodland and grass	13–23 Nov 2016	10	10
Lungwebungu R. 1	-12.580126	18.667396	1,298	Miombo woodland	21–25 Apr 2018	4	1
Lungwebungu R. 2	-12.581990	18.665616	1,208	Miombo woodland	21–25 Apr 2018	4	0
Lungwebungu R. 3	-12.580561	18.664190	1,302	Grassland	21–25 Apr 2018	4	3
Lungwebungu R. 4	-12.578694	18.664674	1,305	Grassland	21–25 Apr 2018	4	0
Lower Quembo R. 1	-13.52801	19.28147	1,236	Marginal grassy vegetation next to river	23–29 Nov 2019	7	1
Lower Quembo R. 2	-13.52816	19.28067	1,240	Miombo woodland	23–29 Nov 2019	7	5
Lower Quembo R. 3	-13.52778	19.27455	1,256	Grassland	23–29 Nov 2019	7	4
Lower Quembo R. 4	-13.25658	19.27810	1,248	Old cultivated lands/ fallow fields	23–29 Nov 2019	7	3
Luanguinga R. 1	-13.70885	21.26234	1,116	Degraded/secondary miombo woodland and grass	1–2 Dec 2019	1	2
Lake Hundo 1	-14.99158	2163096	1,100	Grassland	4–6 Dec 2019	2	1
Lake Hundo 2	-14.97279	21.62890	1,102	Miombo woodland	4–6 Dec 2019	2	0
Lake Hundo 3	-14.97002	21.63139	1,106	Degraded/secondary miombo and grass	4–6 Dec 2019	2	0

Table 2. Species of lizards, chelonians, and crocodiles recorded in the three Angolan Okavango-Cuando-Zambezi River basins. ? = not recorded from the core study area, but expected to occur based on nearby records.

Species	Okavango River Basin	Cuando River Basin	Zambezi River Basin	Source of records
Agamidae				
Acanthocercus cf. *cyanocephalus* (Falk, 1925)	X	X	X	This study; Manaças 1963; Laurent 1964
Acanthocercus margaritae Wagner, Butler, Ceríaco, and Bauer, 2021	X			Monard 1937

Table 2 (continued). Species of lizards, chelonians, and crocodiles recorded in the three Angolan Okavango-Cuando-Zambezi River basins. ? = not recorded from the core study area, but expected to occur based on nearby records.

Species	Okavango River Basin	Cuando River Basin	Zambezi River Basin	Source of records
Agama aculeata Merrem, 1820			X	Monard 1937; Manaças 1963; Laurent 1964
Agama armata Peters, 1855	X		X	This study; Conradie et al. 2016 (as *A. aculeata*)
Agama schacki Mertens, 1938	X			This study
Amphisbaenidae				
Dalophia angolensis Gans, 1976	X		X	Monard 1937; Laurent 1964; Gans 1976
Dalophia ellenbergeri (Angel, 1920)	X	X	X	This study; Branch and McCartney 1992 (as *D. pistillum*)
Dalophia pistillum (Boettger, 1895)	X			Monard 1937
Monopeltis anchietae (Bocage, 1873)	X			Monard 1930, 1937
Monopeltis infuscata Broadley, 1997	X			Broadley et al. 1976
Zygaspis nigra Broadley and Gans, 1969		X	X	This study; Broadley and Gans 1969, 1975
Zygaspis quadrifrons (Peters, 1862)	X	X	X	Monard 1931; Conradie et al. 2016
Chamaeleonidae				
Chamaeleo dilepis Leach, 1819	X	X	X	This study; Mertens 1937; Monard 1937; Manaças 1963; Laurent 1964; Conradie et al. 2016.
Chamaeleo gracilis Hallowell, 1844			X	Laurent 1964
Gekkonidae				
Afroedura wulfhaackei Branch, Schmitz, Lobón-Rovira, Baptista, António, and Conradie, 2021	?			
Chondrodactylus laevigatus (Fischer, 1888)	X			Conradie et al. 2016
Hemidactylus mabouia (Moreau De Jonnès, 1818)	?	?	?	
Hemidactylus nzingae Ceríaco, Agarwal, Marques, and Bauer, 2020	X			Ceríaco et al. 2020a
Lygodactylus angolensis Bocage, 1896	X			This study
Lygodactylus nyaneka Marques, Ceríaco, Buehler, Bandeira, Janota, and Bauer, 2020	X			This study; Conradie et al. 2016 (as *L. bradfieldi*)
Lygodactylus chobiensis FitzSimons, 1932			X	This study
Lygodactylus tchokwe Marques, Ceríaco, Buehler, Bandeira, Janota, and Bauer, 2020			X	Marques et al. 2020
Pachydactylus cf. *punctatus* Peters, 1855	X			This study
Pachydactylus wahlbergii (Peters, 1869)		X		This study
Gerrhosauridae				
Gerrhosaurus auritus Boettger, 1887	X	X	X	This study
Gerrhosaurus cf. *nigrolineatus* Hallowell, 1857	X	X	X	This study; Monard 1937; Conradie et al. 2016
Tetradactylus ellenbergeri (Angel, 1922)	X	X	X	This study; Laurent 1964; Conradie et al. 2016
Lacertidae				
Ichnotropis bivittata Bocage, 1866	X		X	Monard 1937; Manaças 1973
Ichnotropis capensis (Smith, 1838)	X	X	X	This study; Branch and McCartney 1993; Conradie et al. 2016
Ichnotropis cf. *grandiceps* Broadley, 1967	X	X		This study
Heliobolus lugubris (Smith, 1838)	X			Conradie et al. 2016

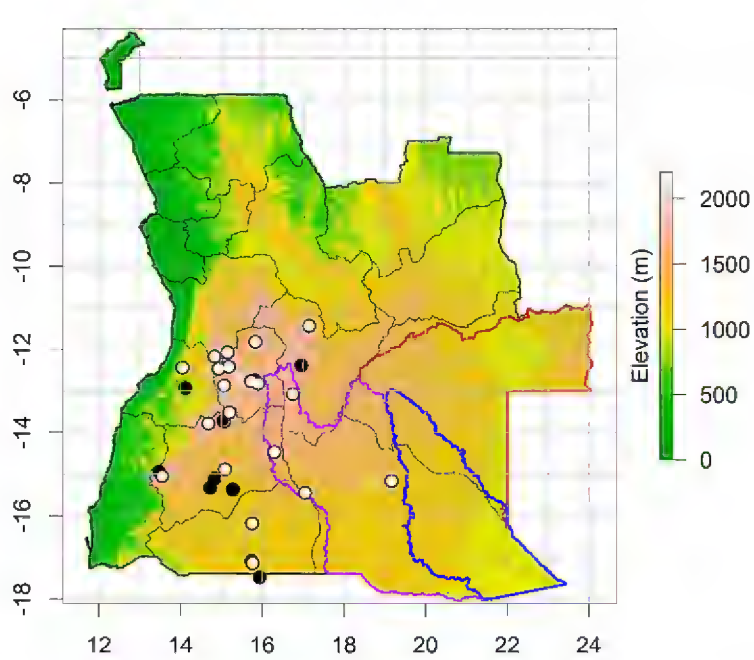
Table 2 (continued). Species of lizards, chelonians, and crocodiles recorded in the three Angolan Okavango-Cuando-Zambezi River basins. ? = not recorded from the core study area, but expected to occur based on nearby records.

Species	Okavango River Basin	Cuando River Basin	Zambezi River Basin	Source of records
Meroles squamulosus (Peters, 1854)	X			This study; Conradie et al. 2016
Nucras scalaris Laurent,1964	X			Baptista et al. 2020
Scincidae				
Acontias jappi Broadley, 1968			X	Broadley 1968
Acontias kgalagadi Lamb, Biswas, and Bauer, 2010		X		Conradie and Bourquin 2013; Conradie et al. 2016
Eumecia anchietae Bocage, 1870	X		X	This study; Monard 1931, 1937
Lubuya ivensii (Bocage, 1879)	X	X	X	This study; Manaças 1963; Conradie et al. 2016
Mochlus sundevallii (Smith, 1849)		X		Conradie et al. 2016
Panaspis maculicollis Jacobsen and Broadley, 2000		X		Conradie et al. 2016
Panaspis wahlbergii (Smith, 1849)	X			Ceríaco et al. 2020
Panaspis sp.	X	X	X	This study
Sepsina angolensis Bocage, 1866	X	X	X	This study; Monard 1931, 1937; Branch and Haagner 1992
Trachylepis albopunctata (Bocage 1867)	X		X	This study; Laurent 1964; Conradie et al. 2016
Trachylepis bayonii (Bocage, 1872)	X	X	X	This study; Monard 1937
Trachylepis chimbana (Boulenger, 1887)			X	Laurent 1964
Trachylepis damarana (Peters, 1870)	X	X	X	This study; Conradie et al. 2016 (as *T. varia*); Weinell and Bauer 2018
Trachylepis punctulata (Bocage, 1872)	X	X	X	This study
Trachylepis spilogaster (Peters, 1882)	X	X		This study; Conradie et al. 2016
Trachylepis sulcata ansorgii (Peters, 1882)	?			
Trachylepis wahlbergii (Peters, 1869)	X	X	X	This study; Conradie et al. 2016
Typhlacontias rohani Angel, 1923	X	X		This study; Angel 1921; Monard 1931; Conradie et al. 2016
Varanidae				
Varanus albigularis (Daudin, 1802)	X			Monard 1937
Varanus niloticus (Linnaeus, 1766)	X			This study; Monard 1937; Manaças 1963; Conradie et al. 2016
Crocodylidae				
Crocodylus niloticus Laurenti, 1768	X	X	X	This study; Monard 1937; Branch and Haagner 1992; Conradie et al. 2016
Order: Testudines				
Pelomedusidae				
Pelomedusa subrufa (Bonnaterre, 1789)	X	X		Monard 1931, 1937; Conradie et al. 2016
Pelusios bechuanicus FitzSimons, 1932		X	X	This study; Laurent 1964; Conradie et al. 2016
Pelusios nanus Laurent, 1956	X	X	X	This study; Monard 1937; Laurent 1964
Pelusios rhodesianus Hewitt, 1827	X	X	X	This study; Monard 1937; Laurent 1964
Testudinidae				
Kinixys belliana Gray, 1863	X		X	This study; Monard 1937; Laurent 1964; Conradie et al. 2016; Kindler et al. 2016
Stigmochelys pardalis (Bell, 1828)		X		Conradie et al. 2016
Species totals: 58	**44**	**29**	**32**	

spp. Large agamid with blue head, chest, and shoulders, mostly in males; 122–148 (133) dorsal scale rows at midbody; 68–74 (71) transverse ventral scales; 78–95 (87) transvers dorsal scales; 11–13 supralabials; 11–15 infralabials; 22–26 (24) subdigital lamellae under 4th toe; 17–35 precloacal pores in 2–3 rows. Largest female: 174.0 + 192.0 mm (PEM R23560); largest male: 137.0 + 162.0 mm (PEM R27387). The new material presented here represents the largest recorded sizes of both male and female for the species (Pietersen et al. 2021; Wagner et al. 2021). **Habitat and natural history notes:** Juveniles were collected in February from the bases of large trees in miombo woodland, while gravid females were collected in October. Adult specimens were found very close to holes in trees, into which they retreated when approached. **Comments:** Wagner et al. (2018) initially assigned all Angolan *Acanthocercus* material to *A. cyanocephalus*, and although they provided a detailed account of Falk's work in Angola, they assigned a specimen from northern Zambia as the neotype, and only examined three Angolan specimens from a single locality. Numerous records of *Acanthocercus* are known across the entire extent of Angola, and recent studies (Marques et al. 2018; Butler et al. 2019) allude to the fact that cryptic species are present in Angola. Follow-up studies (Wagner et al. 2021; Marques et al. 2022b) focused primarily on Namibian and Angolan material and further subdivided this group into three species: *A. margaritae*, ranging from northern Namibia northwards into central and western Angola, *A. ceriacoi* from north-western Angola, and *A. cyanocephalus* from eastern Angola. While these studies made use of integrative taxonomy, they only used a single gene (a fragment of the 16S rDNA) and a small morphological dataset to support their results. The genetic differences among the *Acanthocercus atricollis* group, which includes *A. atricollis*, *A. branchi*, *A. ceriacoi, A. cyanocephalus*, *A. margaritae*, *A. gregorii,* and *A. ugandaensis*, are very small (< 5%) and additional phylogenetic work is needed to support the current taxonomy. Based on geographic proximity, we tentatively assign our material collected from the eastern side of our study area to *A. cyanocephalus*, pending the results of further phylogenetic work.

Acanthocercus margaritae Wagner, Butler, Ceríaco, and Bauer, 2021
Margarita's Tree Agama (Map 2)
Material (1 specimen): PEM R20011, Huambo HALO training site, -12.73722° 15.81825°, 1,670 m asl. **Description:** Juvenile male specimen, measuring 55.9 + 72.0 mm; 120 scale rows at midbody; 76 transvers ventral scales; 76 transverse dorsal scales; 12/13 supralabials; 11/12 infralabials; 24 subdigital lamellae under 4th toe; 18 precloacal pores in two rows. **Habitat and natural history notes:** This specimen was found basking in the early morning on the shade cloth erected around the ablution blocks of the compound. **Comments:** Most historical material from central and western Angola has been reassigned to this recently described species, *A. margaritae* (Wagner et al. 2021). Since our record is from the known distribution of *A. margaritae*, we tentatively assign it to this species, pending further phylogenetic results. This species was not recorded from within the core study area, but based on historical records (Monard 1937), it is expected to occur in the western side of the study area.

Agama armata Peters, 1855
Peter's Ground Agama (Figs. 3–4, Map 3)
Material (12 specimens): PEM R23252, Cacundu falls, -13.77390° 18.75520°, 1,281 m asl; PEM R23310, between Cuchi River to Menongue, -14.67986° 17.17512°, 1,391 m asl; PEM R23319, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23356, Cuito River source lake, grasslands, -12.67756° 18.35589°, 1,495 m asl; PEM R23380, Kuvango River old hydro plant site, -14.38754° 16.30166°, 1,438 m asl; PEM R23391, camp near Malova Village, Mipanha River, -14.09140° 16.41476°, 1,569 m asl; PEM R23407, Lungwebungu River bridge crossing, -12.58346° 18.66598°, 1,304 m asl; PEM R23520, grassland west of Cuanavale River source, -13.01347° 18.81669°, 1,538 m asl; PEM R23994 (iNaturalist 12154222), Aquaculture farm outside Cuito town, -12.439722° 16.89833°, 1,691 m asl; PEM R27388, Luvu River camp, -13.71200° 21.83538°, 1,082 m asl; INBAC: WC-5169, Huambo HALO training site, -12.73726° 15.81828°, 1,665 m asl; INBAC: WC-4574, Lungwebungu River bridge crossing, -12.58347° 18.66598°, 1,294 m asl. **Description:** In juveniles, the ventral scales are more keeled and the ventrum has small, black-edged white circular blotches that seem to fade or disappear with age. The gular region is spotted in both juveniles and adults, although more defined in juveniles. Dorsal scales strongly keeled with nine rows of enlarged scales arranged in longitudinal rows; 89–97 (93) scale rows at midbody; 71–81 (76) transverse ventral scale rows; 45–62 (54) transverse dorsal scale rows; 11–14 supralabials; 10–13 infralabials;

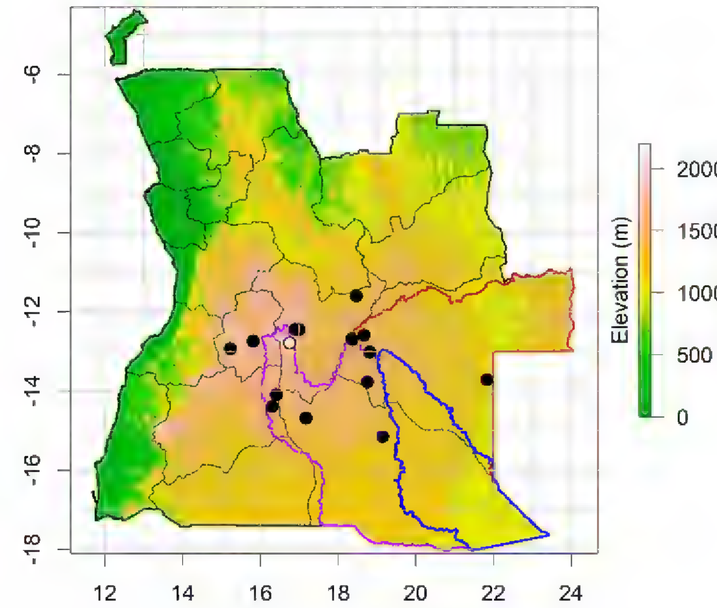


Map 2. Distribution of *Acanthocercus margaritae* in Angola.

Fig. 3. Adult male *Agama armata* (PEM R23252) from Cacundu Falls. *Photo by Werner Conradie*.

Fig. 4. Gravid female *Agama armata* (PEM R27388) from Luvu River camp. *Photo by Chad Keates*.

15–18 (16) subdigital lamellae under 4th toe; 10–12 precloacal pores in a single row. Largest female: 88.5 + 95.0 mm (INBAC: WC-4574); largest male: 85.9 + 113.0 mm (PEM R23380, new maximum size). **Habitat and natural history notes:** Juveniles were collected in February, while gravid females were collected in October. **Comments:** Species identification was based on the gular pattern (spotted versus striped in *A. aculeata*) as documented by Jacobsen (1992). Re-examination of a specimen recorded as *A. aculeata* from north of Cachingues in Conradie et al. (2016) also conforms to this species. Although some historical Angolan material was referred to *A. armata* (see Bocage 1895; Boulenger 1905), Marques et al. (2018) regarded all material from Angola as *A. aculeata*, and mention that *A. armata* is 'extralimital' and restricted to southeastern South Africa. In contrast, *A. armata* has been regularly documented from adjacent Zambia (Broadley 1971; Pietersen et al. 2017, 2021; Bittencourt-Silva 2019). All available historical Angolan material under the names *A. aculeata* and *A. armata*, especially those from eastern Angola (Manaças 1963; Laurent 1964), needs to be re-examined to establish the true identification and full extent of the ranges of these two species in Angola. It is noteworthy that members of the *Agama aculeata-armata* group are genetically similar, which may necessitate the synonymy of these species in the future (Leaché et

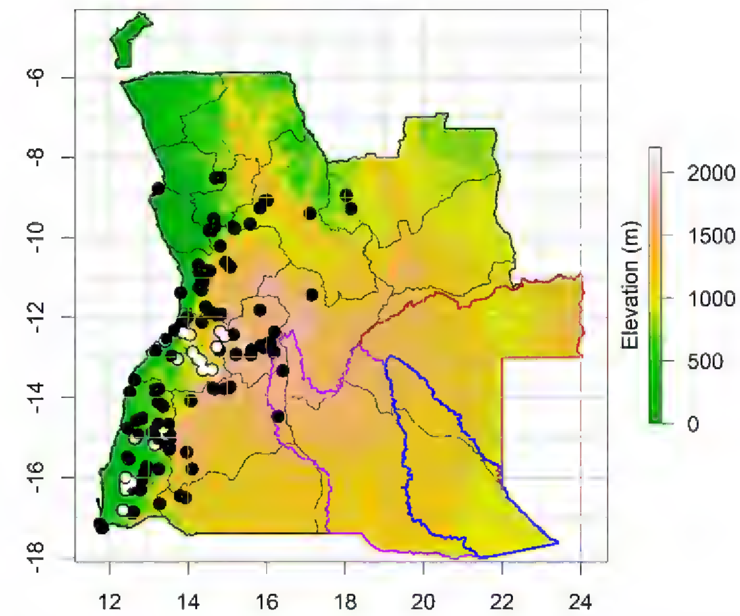


Map 3. Distribution of *Agama armata* in Angola.

al. 2014). If the specific status of these two species is confirmed, then both might be present in Angola, with *A. aculeata* restricted to the more arid western regions of Angola and *A. armata* to the more mesic eastern regions.

Agama schacki Mertens, 1938
Schack's Rock Agama (Fig. 5, Map 4)
Material (16 specimens): PEM R23367, en route to Cuito, east of Huambo, -12.73615° 15.97442°, 1,777 m asl; PEM R23381–7, INBAC: WC-5208–9, campsite near old Cuvango Mission on Cubango River, -13.32887° 16.41167°, 1,520 m asl; PEM R23395–400, INBAC: WC-5162, Cubango River near source, -12.66256° 16.09324°, 1,764 m asl. **Description:** Large, rupicolous agama. Male with orange head and tail; 84–101 (92) scale rows at midbody; 80–94 (88) transverse ventral scale rows; 71–80 (74) transverse dorsal scale rows; 9–11 supralabials; 9–12 infralabials; 21–24 (22) subdigital lamellae under 4th toe; 11–13 precloacal pores in a single row. Largest female: 102.3 + 142.0 mm (PEM R23383); largest male: 118.0 + 95t mm (PEM R23387 had the longest intact tail which measured 173 mm [1.5 x SVL]). **Habitat and natural history notes:** Individuals were associated with large rocky outcrops, especially along the upper Cubango River. **Comment:** Based on the higher midbody scale counts, we can confidently assign our material to the *A. schacki* group (Mertens 1938). Ignoring the erroneous records of Monard (1937) from Cuando Cubango Province, our material represents the most easterly records for this species. The status of the Angolan Rock Agamas was briefly discussed by Ceríaco et al. (2014). Preliminary phylogenetic results indicate that *A. schacki* should be treated as a full species, and that more cryptic species are present in the larger Angolan Rock Agama group (Marques et al. 2018; Butler 2020). We follow these studies and treat *A. schacki* as a distinct species from *A. planiceps*, restricting the latter to the arid regions of the Namibe Province, and we treat all other records as *A.* aff. *schacki* until the taxonomic status of the cryptic species are addressed. Butler (2020) lacked genetic material from central Angola, and our material may potentially represent either of the two inland clades identified in that study. Since efforts

Fig. 5. Adult male *Agama schacki* (PEM R23367) from near source of the Cubango River. *Photo by Werner Conradie.*



Map 4. Distribution of *Agama planiceps* complex in Angola.

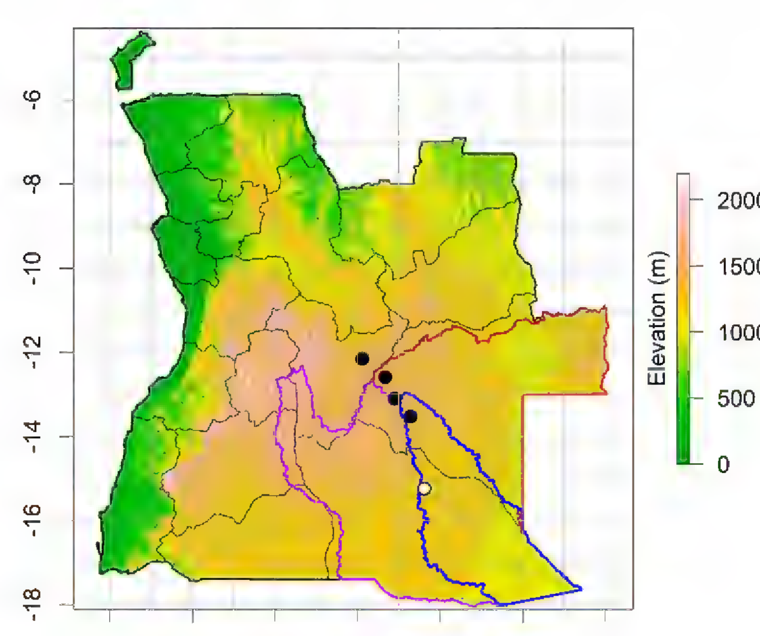
to separate the species in the *Agama planiceps* complex are still ongoing, we produced a map for the entire species complex (Map 4).

Amphisbaenidae

Dalophia ellenbergeri (Angel, 1920)
Ellenberger's Worm Lizard (Fig. 6, Map 5)
Material (4 specimens): PEM R23408, Lungwebungu River camp bridge crossing, -12.58346° 18.66598°, 1,304 m asl; PEM R23492, Cuanavale River source lake, -13.09442° 18.89372°, 1,396 m asl; PEM R24002, 5 km west of Cuemba, -12.14751° 18.11650°, 1,329 m asl; PEM R27392, Quembo River bridge camp, -13.52745° 19.2806°, 1,241 m asl. **Description:** All specimens exhibit the diagnostic 'herringbone' scale arrangement on the dorsal side of the tail; 16–21 dorsal segments per body annulus; 12–14 ventral segments per body annulus; 309–319 body annuli; 29–43 caudal annuli; caudal autonomy site at the 8th caudal annulus; 3–4 supralabials; 3 infralabials. Largest specimen: 336.0 + 76.0 mm (PEM R27392). **Habitat and natural history notes:** All specimens were excavated from sandy soils, except for one individual that was found on the surface after heavy rain and another which was found taking refuge under a tree log. **Comments:** Angola has one of the richest assemblages of amphisbaenians in Africa, represented by three genera and 11 species (Marques et al. 2018). The taxonomy of Angolan amphisbaenians has a turbid history, and many of the species have not been evaluated in a phylogenetic framework. The only phylogenetic study on African amphisbaenians incorporated only one Angolan sample (Measey and Tolley 2013). *Dalophia ellenbergeri* was first reported from Angola by Branch and McCartney (1992) under the name *D. pistillum* and later re-identified as *D. ellenbergeri* (Broadley 1997). This is only the second time this species has been recorded from Angola and it is now documented from four additional localities. Elsewhere it is only recorded from western Zambia (Broadley 1971; Pietersen et al. 2021).

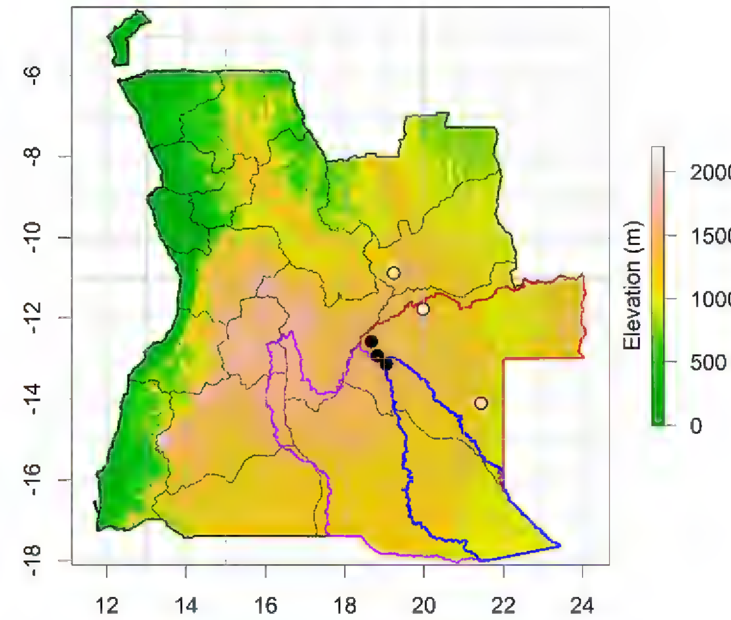
Fig. 6. Adult *Dalophia ellenbergeri* (PEM R23408) from Lungwebungu River. *Photo by Werner Conradie.*

Zygaspis nigra Broadley and Gans, 1969
Black Round-headed Worm Lizard (Fig. 7, Map 6)
Material (3 specimens): PEM R23564–5, Samanunga village, -12.93250° 18.81476°, 1,363 m asl; PEM R23984, Lungwebungu River crossing, -12.58020° 18.66773°, 1,298 m asl. **Additional records:** Quembo River source, -13.13586° 19.04709°, 1,368 m asl (stomach contents of *Xenocalamus mechowii* – PEM R23463). **Description:** Male (PEM R23564) with four precloacal pores; hemipenis bifurcated and extending to 6–7th caudal annuli. Female (PEM R23564) with



Map 5. Distribution of *Dalophia ellenbergeri* in Angola.

Fig. 7. Adult *Zygaspis nigra* (PEM R23564) from Samanunga village. *Photo by Werner Conradie.*



Map 6. Distribution of *Zygaspis nigra* in Angola.

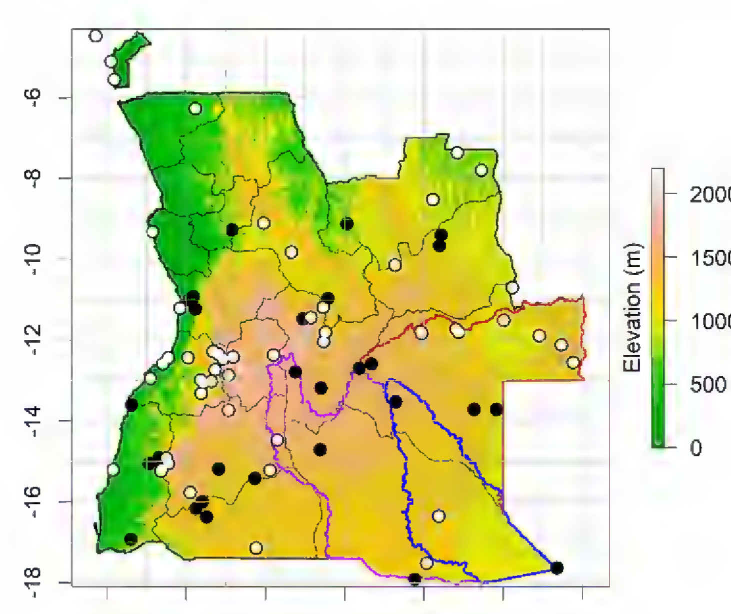
truncated tail at 7th annulus. Adults have distinct black bars, while juveniles are much lighter in color; 16–17 dorsal segments per body annulus; 12 ventral segments per body annulus; 189–194 body annuli; 42–43 caudal annuli, caudal autonomy site at 7th caudal annulus; 3 supralabials; 3 infralabials. Largest female: 216.0 + 8t mm (PEM R23565); largest male: 232.0 + 41.0 mm (PEM R23564). **Habitat and natural history notes:** One female contained three elongated eggs (20 x 5 mm). Two specimens were excavated by local farmers while preparing agricultural fields. **Comments:** Only two species of *Zygaspis* are known from scattered records in southern and eastern Angola (Marques et al. 2018; Baptista et al. 2019; Butler et al. 2019). *Zygaspis nigra* was originally described from western Zambia, with only a few records from eastern Angola and the Zambezi Region in northeastern Namibia (Broadley and Gans 1969; Pietersen et al. 2021). Historically this species is only known from three localities in eastern Angola (Marques et al. 2018), so these new records double the number of known localities from Angola.

Chamaeleonidae

Chamaeleo dilepis Leach, 1819 complex
Flap-necked Chameleon (Fig. 8, Map 7)

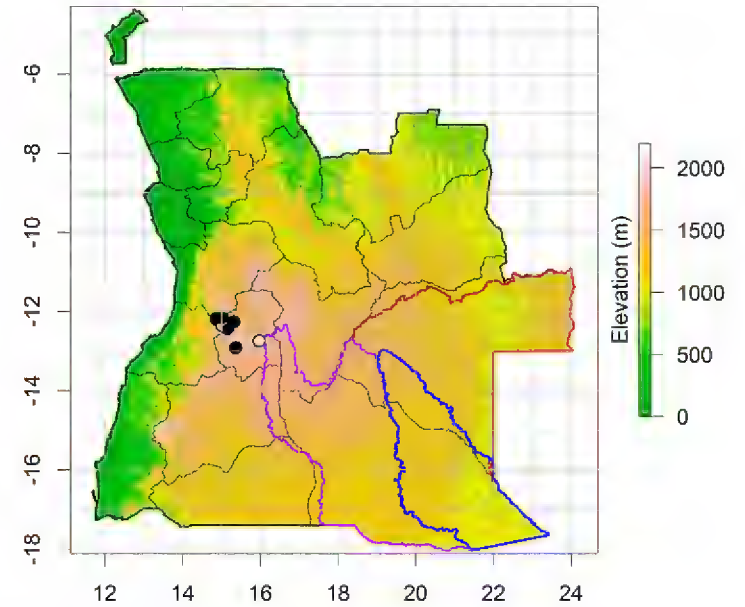
Fig. 8. Adult female *Chamaeleo dilepis* (not collected) from lower Quembo River. *Photo by Werner Conradie.*

Material (5 specimens): PEM R23322, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R27391, Luvu River camp, -13.71200° 21.83538°, 1,082 m asl; PEM R27389–90, INBAC: WC-6789, Lungwebungu River camp, -12.58439° 18.66748°, 1,297 m asl. **Additional observations:** Quembo River, walk back from small waterfall, -13.52987° 19.28340°, 1,242 m asl; Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28486°, 1,248 m asl; Camp at side tributary (Luandai River) of the Luanguinga River, -13.70885° 21.26234°, 1,116 m asl; Cuelei River west of Menongue, -14.70511° 17.38014°, 1,392 m asl; Chitembo, -12.78792° 16.75706°, 1,693 m asl. **Description:** All specimens presented a small, reduced occipital flap. Largest female: 97.1 + 84.0 mm (PEM R27391); largest male: 88.5 + 95.0 mm (PEM R23322). **Habitat and natural history notes:** All adult specimens were encountered sleeping at night in larger trees up to a height of 2 m, while hatchlings were found very low on scrub below 30 cm height. A gravid female (photographed and released) was found at the Cuito River source in February. **Comment:** Although the casques and occipital lobes of our material seem very reduced (a feature diagnostic of *C. gracilis*), the tail is long and the dorsal keel is formed by a single row of enlarged tubercles (double in *C. anchietae*), conforming to typical



Map 7. Distribution of *Chamaeleo dilepis* in Angola.

Fig. 9. Adult female *Afroedura wulfhaackei* (PEM R22490) from 1 km west of Candumbo on road to Boas Águas. *Photo by Luke Verburgt*.



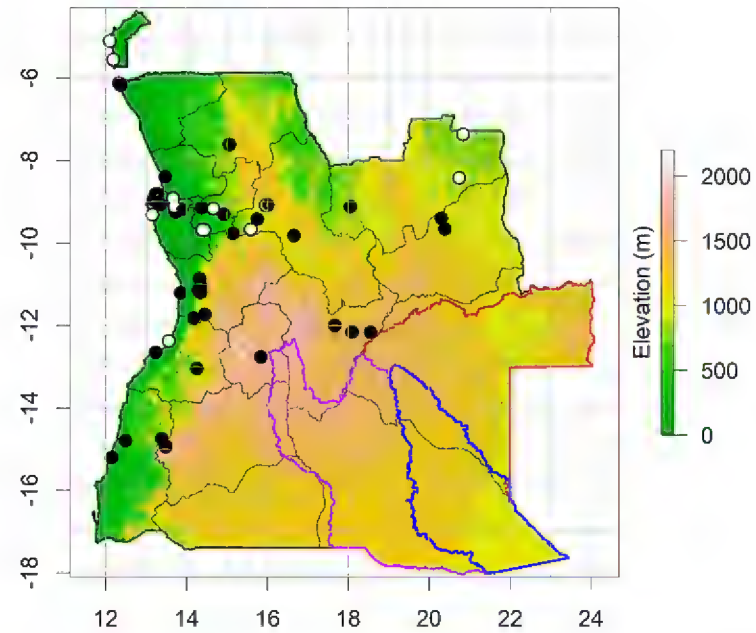
Map 8. Distribution of *Afroedura wulfhaackei* in Angola.

C. dilepis features (Tilbury 2010, 2018). Chameleons are very poorly represented in Angola, with only two genera and five species recorded (Marques et al. 2018). Of these, *C. dilepis* is the most common and widespread (Marques et al. 2018), although only a few records are known from the southeast (Conradie et al. 2016). The new records presented here fill the sampling gap in the distribution of this species in Angola. Numerous subspecies and variations have been described in this group over the years (Uetz et al. 2022), but a recent large-scale phylogenetic study (Main et al. 2022) identified only three species-level lineages that do not fully agree with previously identified subspecies. Of these lineages, two occur in Angola, but due to the lack of topotypic material and the fact that the recognized lineages are incongruent with previously described subspecies, further studies are recommended for this taxon. We therefore refer to our collected material by the binominal name.

Gekkonidae

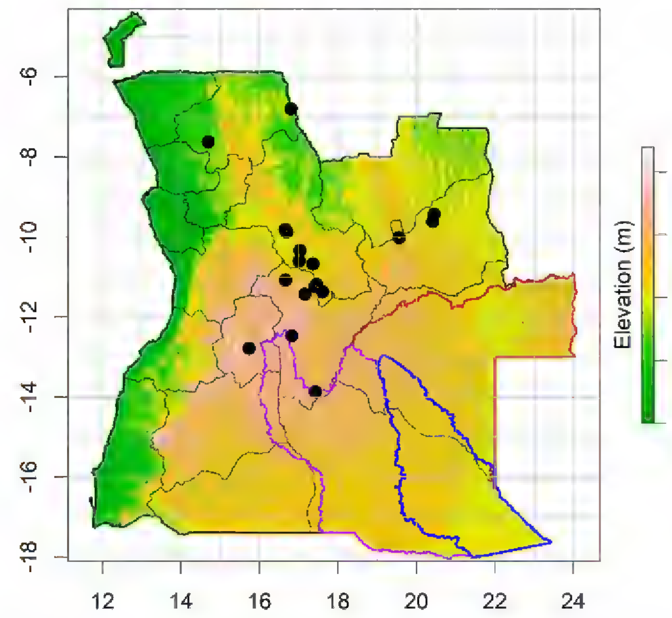
Afroedura wulfhaackei Branch, Schmitz, Lobón-Rovira, Baptista, António, and Conradie, 2021
Angolan Flat Gecko (Fig. 9, Map 8)
Material (3 specimens): PEM R22490–1, PEM R24200, Candumbo Rocks Memorial, -12.73614° 15.97442°, 1,777 m asl. **Description:** 77–79 dorsal midbody scale rows; 8–9 supralabials; 8 infralabials; 7–8 enlarged scales under 4th toe; 4 ventral verticils and 5 dorsal verticils per tail whorl. Largest female: 54.4 + 0t mm (PEM R 22491). **Habitat and natural history notes:** Found under exfoliating rocks among larger rock boulders. **Comment:** These represent the most inland records of this recently described species (Branch et al. 2021). Although this species was not documented from within the defined core study area of this project, suitable habitat is found along the northern and western edge of the study area.

Hemidactylus mabouia (Moreau de Jonnès, 1818)
Common Tropical House Gecko (Map 9)
Material (3 specimens): PEM R24001, Cuemba town, -12.14786° 18.09100°, 1,351 m asl; PEM R23558, Munhango village, -12.16445° 18.5548°, 1,435 m asl; PEM R23377, Kwanza River bridge, -11.99348° 17.66965°, 1,727 m asl. **Description:** Subcaudal scales enlarged and elongated; 88–89 dorsal midbody scale rows; 16–17 longitudinal rows of enlarged keeled tubercles; 34 ventral midbody scale rows; 10 supralabials; 9–10 infralabials; 6–7 divided scansors under 4th toe; 14/15 precloacal pores in a single row. Largest female: 52.6 + 61.0 mm (PEM R23558); largest male: 53.5 + 62.0 mm (PEM R24001). **Habitat and natural history notes:** All specimens were found on or near anthropogenic structures. **Comment:** The species is present across most of Angola, but has not yet been recorded from extreme southeastern Angola (Marques et al. 2018; Ceríaco et al. 2020a; Lobón-Rovira et al. 2021). Due to its high human-assisted dispersal capacity and adaptation to anthropogenic structures (Agarwal et al. 2021), this species is expected to spread to larger towns and settlements in southeastern Angola. A recent large-scale phylogenetic study revealed at least 20 species-level lineages, with most Angolan material corresponding to the *H. mabouia sensu stricto* lineage (Agarwal et al. 2021).



Map 9. Distribution of *Hemidactylus mabouia* in Angola.

Fig. 10. Adult male *Hemidactylus nzingae* (PEM R23991) from Cuquema River. *Photo by Werner Conradie.*



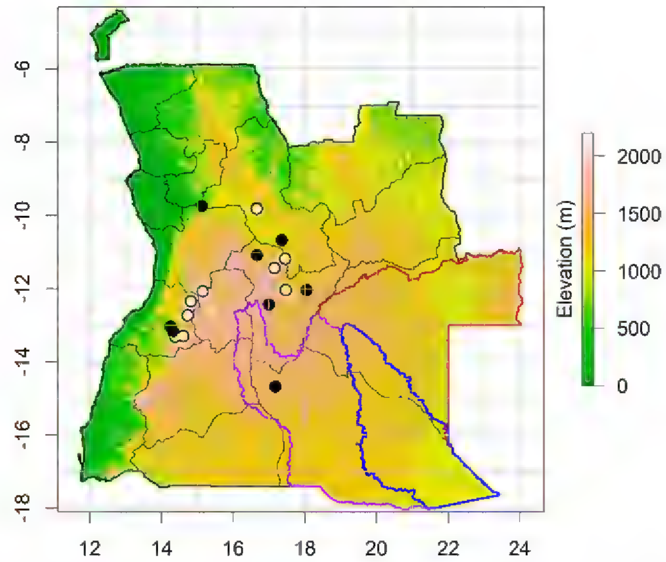
Map 10. Distribution of *Hemidactylus nzingae* in Angola.

Hemidactylus nzingae Ceríaco, Agarwal, Marques, and Bauer, 2020
Queen Nzinga's Tropical Gecko (Fig. 10, Map 10)
Material (2 specimens): PEM R23990 (iNaturalist 12128372), Rio Cuquema, downstream, -12.47021° 16.82334°, 1,644 m asl; PEM R23991, Rio Cuquema, upstream, -12.46902° 16.82415°, 1,640 m asl. **Description:** 58–66 dorsal midbody scale rows; 16 longitudinal rows of enlarged keeled tubercles; 25 ventral midbody scale rows; 9–10 supralabials; 8–9 infralabials; 7 divided scansors under 4th toe; 3/3 precloacal pores in a single row. Largest male: 40.2 + 37.9 mm (PEM R23991). **Habitat and natural history notes:** Specimens were found actively running on the ground during the day. **Comment:** This species was only recently described and seems to be common in miombo woodland on the Angolan plateau (Ceríaco et al. 2020a; Lobón-Rovira et al. 2021). In a follow-up study, 'unpatterned' specimens that occur sympatrically with *H. nzingae* were described as a new species, *H. hannahsabinae* (Ceríaco et al. 2020b). The addition of more material, with some from this study including these 'unpatterned' specimens, showed that the latter taxon is a junior synonym of *H. nzingae* (Lobón-Rovira et al. 2021).

Lygodactylus angolensis Bocage, 1896
Angolan Dwarf Day Gecko (Fig. 11, Map 11)
Material (3 specimens): PEM R23311, drive back from Cuchi to Menongue, -14.67986° 17.17512°, 1,391 m asl; PEM R23343, 10 km west of Cuemba village, -12.03481° 18.04869°, 1,437 m asl; PEM R23995 (iNaturalist 12123557), south of Cuito town, -12.43930° 16.99143°, 1,624 m asl. **Description:** Mental divided by a pair of lateral clefts; 81–87 (84) dorsal midbody scale rows; 21–22 ventral midbody scale rows; 7–8 supralabials; 7–8 infralabials; 2–3 scales touching nostril; 4 divided scansors under 4th toe; 9 precloacal pores in a V-shape. Largest female: 29.8 + 34.0 mm (PEM R23995); largest male: 30.1 + 34.6 mm (PEM R23311). **Habitat and natural history notes:** Found on tree trunks during the day in miombo woodland. **Comment:** Assigned to *L. angolensis* based on the high number of precloacal pores (9) and the number of scales touching the nostril (~3; Marques et al. 2020). One specimen (PEM R23312) was found in sympatry with *L. nyaneka* and constitutes the southernmost Angolan record and the first from Cuando Cubango Province.

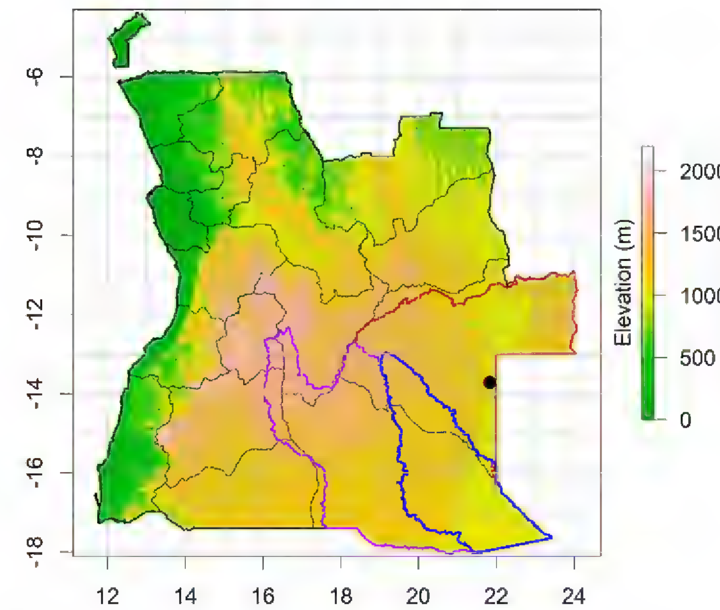
Lygodactylus chobiensis FitzSimons, 1932
Okavango Dwarf Gecko (Fig. 12, Map 12)
Material (1 specimen): PEM R27402, Luvu River camp, -13.71200° 21.83538°, 1,082 m asl. **Description:** Mental

Fig. 11. Adult female *Lygodactylus angolensis* (PEM R23995) from south of Cuito town. *Photo by Alex Rebelo.*



Map 11. Distribution of *Lygodactylus angolensis* in Angola.

Fig. 12. Adult female *Lygodactylus chobiensis* from Luvu River. *Photo by Chad Keates.*



Map 12. Distribution of *Lygodactylus chobiensis* in Angola.

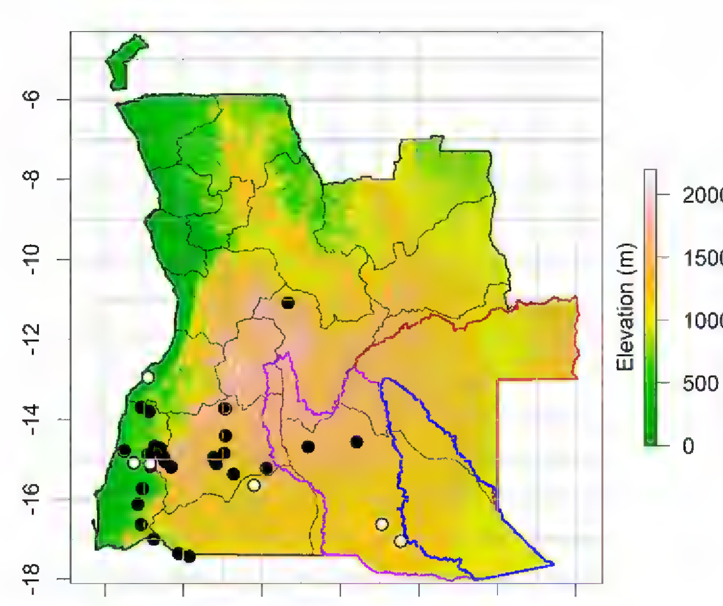
not divided by lateral clefts, two faint dark V-shaped chevrons on throat; 74 dorsal midbody scale rows; 22 ventral midbody scale rows; 6/6 supralabials; 6/6 infralabials; 4 scales touching nostril; 5 divided scansors under 4th toe. Largest female: 25.5 + 26.2 mm (PEM R27402). **Habitat and natural history notes:** Found sleeping in a tree at night. **Comment:** This represents the first documented record for Angola, although this species has been predicted to occur in eastern and southeastern Angola (Marques et al. 2018).

Lygodactylus nyaneka Marques, Ceríaco, Buehler, Bandeira, Janota, and Bauer, 2020
Nyaneka Dwarf Gecko (Fig. 13, Map 13)
Material (2 specimens): PEM R23312, drive back from Cuchi to Menongue, -14.67986° 17.17512°, 1,391 m asl; PEM R23540, Longa River, -14.55956° 18.41389°, 1,320 m asl. **Description:** Mental divided by a pair of lateral clefts; 83 and 93 dorsal midbody scale rows; 16 and 22 ventral midbody scale rows; 7–8 supralabials; 7–8 infralabials; 3–4 scales touching nostril; 4 divided scansors under 4th toe; 6 precloacal pores in a V-shape. Largest female: 32.4 + 30.3 mm (PEM R23540); largest male: 35.2 + 17.4t mm (PEM R23312). **Habitat and natural history notes:** Found in miombo woodland. **Comment:** We tentatively assign our new material, including the material reported as *L. bradfieldi* by Conradie et al. (2016), to this species based on shared morphological characters (number of scales touching the nostril and low number of precloacal pores, Marques et al. 2020) until further phylogenetic studies are conducted.

Pachydactylus cf. *punctatus* Peters, 1854 complex
Speckled Thick-toed Gecko (Fig. 14, Map 14)
Material (2 specimens): PEM R23262, Cuchi River gorge, -14.59000° 16.90758°, 1,350 m asl; PEM R23537, Cuchi River gorge, -14.58983° 16.90744°, 1,364 m asl. **Description:** Specimens are light brown above with fine white speckles; 74 and 76 midbody scale rows; 6–7 supralabials; 8–6 infralabials; 4 undivided scansors under 4th toe. Largest female 33.8 + 32.7 mm (PEM R23262); largest male: 34.7 + 25.8t mm (PEM R23537). **Habitat and natural history notes:** Specimens were found active at night on rock surfaces adjacent to Cuchi River gorge. **Comment:** The taxonomic status of this species complex is currently under revision and it may represent multiple cryptic lineages (H. M. Heinz, unpub. data).

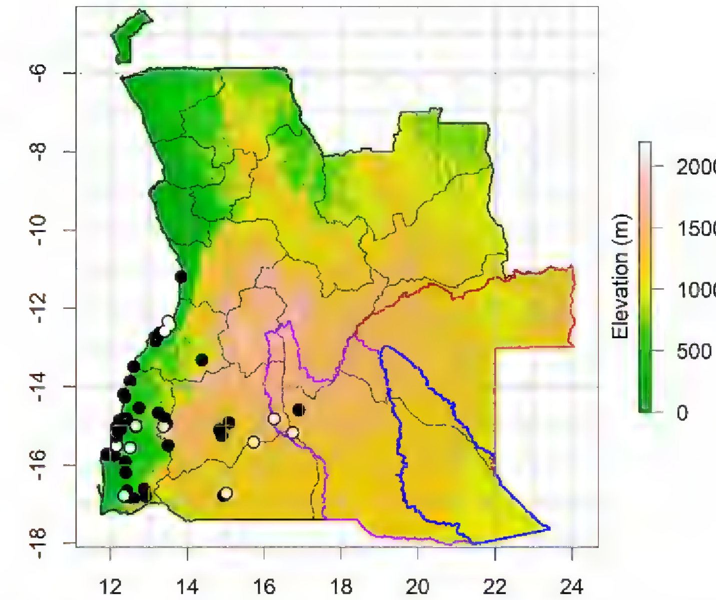
Pachydactylus wahlbergii (Peters, 1869)
Kalahari Ground Gecko (Fig. 15, Map 15)
Material: PEM R25083, Cuando River, CUD2018 AC Camp 22, -15.82175° 21.58647°, 1,050 m asl.

Fig. 13. Adult male *Lygodactylus nyaneka* (PEM R23312) from west of Menongue. *Photo by Werner Conradie.*



Map 13. Distribution of *Lygodactylus nyaneka* in Angola.

Fig. 14. Adult female *Pachydactylus* cf. *punctatus* (PEM R23262) from Cuchi River gorge. *Photo by Werner Conradie.*



Map 14. Distribution of *Pachydactylus punctatus* complex in Angola.

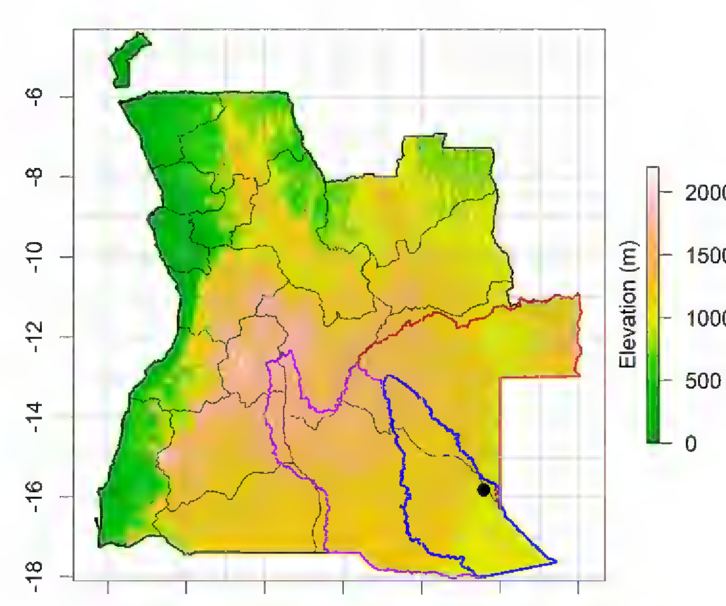
Description: 72 midbody scale rows; 7/8 supralabials; 6/6 infralabials; 2 undivided scansors under 4^{th} toe. Largest male: 25.5 + 26.2 mm (PEM R25083). **Habitat and natural history notes:** Found beneath a tent pitched on the sandy bank adjacent to the Cuando River. **Comment:** Although Haacke (1976) recorded this species from the border between Angola and Namibia, no official records have been documented from Angola. This therefore represents the first confirmed record for Angola. This new record is unsurprising, given the recent record of this species in western Zambia (Pietersen et al. 2017).

Gerrhosauridae

Gerrhosaurus auritus Boettger, 1887
Kalahari Plated Lizard (Fig. 16, Map 16)
Material (7 specimens): PEM R23273, Cuanavale River source, -13.09330° 18.89396°, 1,367 m asl; PEM R23313, drive to Quemba village on grasslands, -12.14597° 18.39728°, 1,402 m asl; PEM R23324, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23481, Cuando River source, trap 4, -13.00164° 19.1296°, 1,372 m asl; PEM R23557, DOR en route from Munhango to Cuanavale River source, -12.56364° 18.66669°, 1,317 m asl; PEM R23974 (iNaturalist 12410724), Lungwebungu River, ad hoc, -12.58619° 18.66538°, 1,300 m asl; PEM R23975 (iNaturalist 12410714), Lungwebungu River new campsite, -12.58445° 18.66538°, 1,308 m asl. **Description:** No dorsolateral yellow stripe; flanks with scattered orange scales; tympanic shield very broad and crescentic; weak to moderately keeled lateral scales; scales on soles of feet keeled; 26–28 (26) dorsal midbody scale rows; 8 enlarged ventral plates; 50–52 (51) transverse ventral scale rows; 3 supralabials; 3–4 infralabials; 4–5 supraciliaries; 16–18 (17) subdigital lamellae under 4^{th} toe; 13–17 (15) femoral pores per thigh. Largest female: 156.0 + 254.0 mm (PEM R23557); largest male: 143.5 + 249.0 mm (PEM R23273). **Habitat and natural history notes:** Found active during the day in close proximity to their burrows in miombo woodland or grasslands, to which they retreated when disturbed. **Comment**: Although a historical record exists from Lunda Sul Province (Monard 1937), these are the first modern records of this species for Angola. The species has also been recorded from adjacent western Zambia (Pietersen et al. 2017).

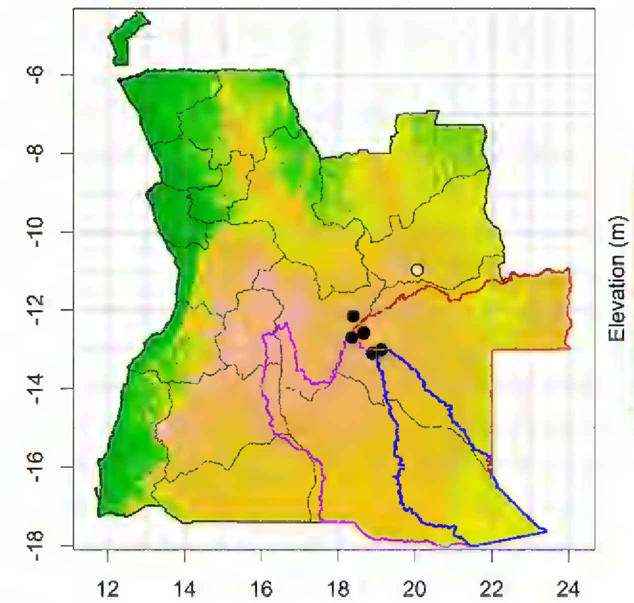
Gerrhosaurus cf. *nigrolineatus* Hallowell, 1857 complex
Black-lined Plated Lizard (Fig. 17, Map 17)

Fig. 15. Adult male *Pachydactylus wahlbergii* (PEM R25083) from middle Cuando River. *Photo by Götz Neef.*



Map 15. Distribution of *Pachydactylus wahlbergii* in Angola.

Fig. 16. Adult male *Gerrhosaurus auritus* (PEM R23273) from Cuanavale River source. *Photo by Werner Conradie*.

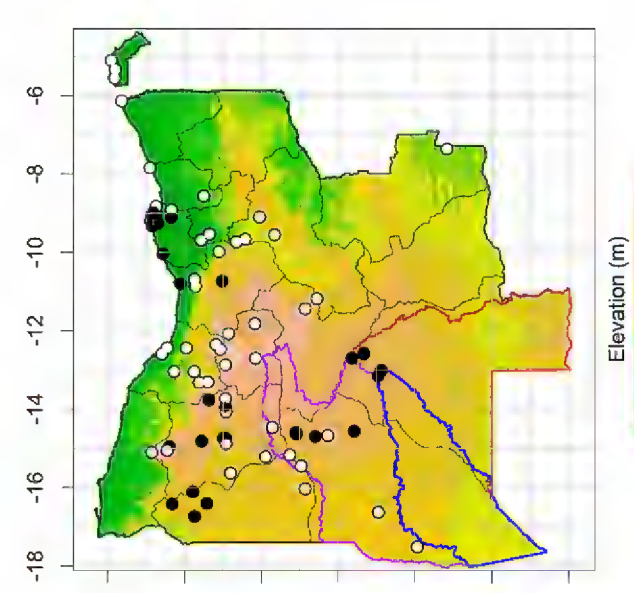


Map 16. Distribution of *Gerrhosaurus auritus* in Angola.

Material (10 specimens): PEM R23260, R23302, Cuchi River gorge, -14.5900° 16.90758°, 1,350 m asl; PEM R23324–5, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23447, Cuando River source, trap 3, -13.00334° 19.13564°, 1,364 m asl; PEM R23534, EN280 west of Menongue, -14.68908° 17.41242°, 1,454 m asl; PEM R23541, Longa River, -14.55942° 18.41431°, 1,321 m asl; PEM R23544–5, Quembo River source camp, -13.14557° 19.04571°, 1,423 m asl; PEM R23973, Lungwebungu River, ad hoc, -12.58619° 18.66538°, 1,300 m asl; PEM R23988, Lungwebungu River, ad hoc, -12.56806° 18.66639°, 1,294 m asl. **Description:** Distinct dorsolateral yellow stripe and bright orange flanks with yellow spots; tympanic shield narrow; weak to moderately keeled lateral scales; scales on soles of feet smooth; 23–24 (24) dorsal midbody scale rows; 8 enlarged ventral plates; 49–51 (50) transverse ventral scale rows; 3 supralabials; 3 infralabials; 4 supraciliaries; 15–18 subdigital lamellae under 4th toe; 15–20 (16) precloacal pores per thigh. Largest female: 150.9 + 233.0 mm (PEM R23544); largest male: 139.0 + 277.0 mm (PEM R23325). **Habitat and natural history notes:** Found sympatrically with *G. auritus* at certain localities, e.g., Cuito River source and Lungwebungu River bridge site. *Gerrhosaurus* cf. *nigrolineatus* utilizes the same habitats as *G. auritus* and exhibits similar behavior. **Comment:** A species with a wide distribution in Africa and in Angola (Marques et al. 2018). Eastern African populations of *G. nigrolineatus* were re-assigned to *G. intermedius* by Bates et al. (2013), and the status of the Angolan north-central and western populations of *G. multilineatus*, as well as their relationships within the *G. nigrolineatus* complex in Angola, are under investigation (M. Bates, pers. comm.).

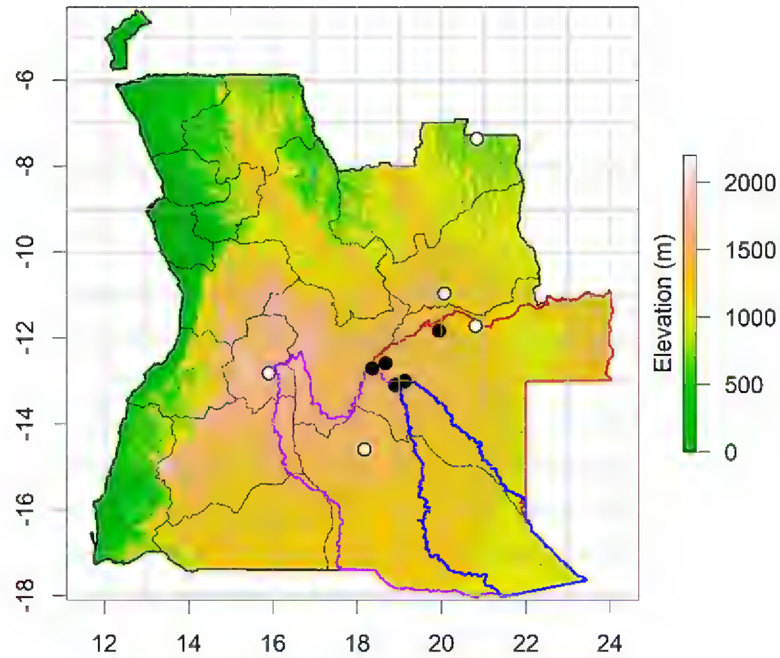
Tetradactylus ellenbergeri (Angel, 1922)
Ellenberger's Long-tailed Seps (Fig. 18, Map 18)
Material (4 specimens): PEM R23375 (neonate), outlet of Cuito River source lake, -12.70453° 18.35445°, 1,429 m asl; PEM R23424, Cuando River source, -13.00345° 19.12751°, 1,343 m asl; PEM R23976 (posterior half of body and tail only), Lungwebungu River campsite, -12.58319° 18.66573°, 1,284 m asl; PEM R24275, Cuanavale River source lake, -13.09442° 18.89372°, 1,397 m asl. **Description:** Dorsal scales ridged with a central keel; 12–14 dorsal midbody scale rows; 6 enlarged longitudinal ventral plates; 63 transverse ventral scale rows; 63 transverse dorsal scale rows; 4 supralabials; 3 infralabials; 3 supraciliaries; no front limbs; hind limbs monodactyle (< 2 mm). Largest specimen: 62.5 + 160.0

Fig. 17. Adult male *Gerrhosaurus* cf. *nigrolineatus* (PEM R23325) complex from Cuito River source. *Photo by Werner Conradie*.



Map 17. Distribution of *Gerrhosaurus nigrolineatus* complex in Angola.

Fig. 18. Adult female *Tetradactylus ellenbergeri* (PEM R23424) from Cuando River source. *Photo by Werner Conradie.*



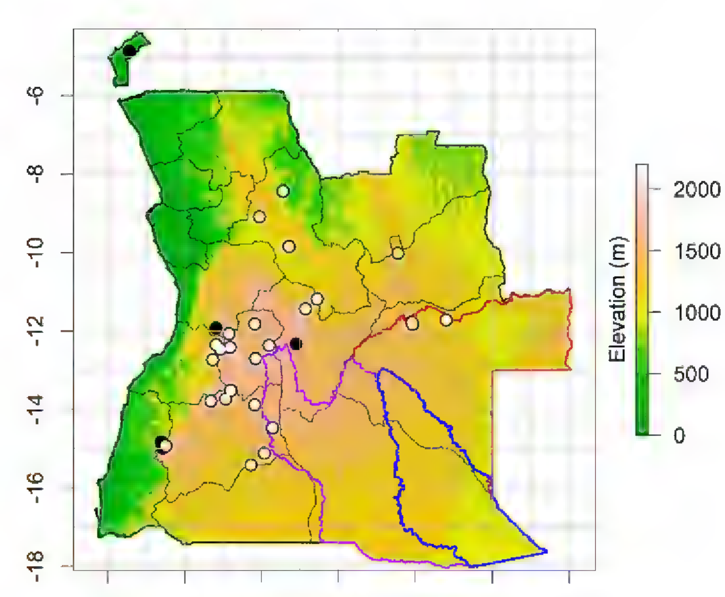
Map 18. Distribution of *Tetradactylus ellenbergeri* in Angola.

mm (PEM R24275). **Habitat and natural history notes:** All specimens were found near waterbodies. One female specimen (PEM R23424) was captured by a Cattle Egret (*Bubulcus ibis*) that released the specimen upon being startled. The specimen contained two eggs (8.4 x 3.5 mm) in November. One neonate (PEM R23375) was collected at the outlet of the Cuito River source lake in February. **Comment:** These new records fill the gap between the most southeastern Luassinga River record (Conradie et al. 2016) and the northeastern Angolan records (Monard 1937; Laurent 1964), and they are the first records for the Cuando River basin. The taxonomy of this species in Angola has been complicated by the naming of *T. lundensis* Monard, 1937 and *T. fitzsimonsi simplex* Laurent, 1950. Laurent (1964) synonymized these two species with *T. boulengeri*, which he in turn separated from *T. ellenbergeri* based on the lower number of dorsal scale rows (12 versus 14). Broadley (1971) rejected this, as he found specimens in eastern Zambia whose dorsal scale rows varied from 12–14 (the outer scale rows being much smaller). Most of our specimens had 12 dorsal scale rows, except for two specimens from the Cuando River (PEM R23424) and the Luassingua River (Conradie et al. 2016), which each had 14 dorsal scale rows (outer scale rows half the size of adjacent rows).

Lacertidae

Ichnotropis bivittata Bocage, 1866
Angolan Rough-scaled Lizard (Fig. 19, Map 19)
Material (1 specimen): PEM R23530, west of Cuito town on Aludungo road, -12.32784° 16.90673°, 1,742 m asl. **Description:** 35 midbody scale rows; 10 longitudinal rows of enlarged ventral plates; 31 transverse ventral scale rows; 4/4 supralabials; 6/6 infralabials; 4/4 supraciliaries; 19 subdigital lamellae under 4th toe; 10/10 femoral pores per thigh. Largest female: 59.9 + 98.0 mm (PEM R23530). **Comment:** Collected outside of the core study area, but it contributes to the distributional data for both the species and the region. Laurent (1964) described *I. b. pallida* from Huíla based on duller coloration and minor differences in head scalation. Recently, Butler et al. (2019) and Bandeira (2019) erroneously referred material from Bicuar National Park to *I. b. pallida*, but these are actually subadult non-breeding *I. capensis* (see Baptista et al. 2019 and the following species account). Bandeira

Fig. 19. Adult female *Ichnotropis bivittata* (PEM R23530) from west of Cuito town on the Aludungo road. *Photo by Werner Conradie.*

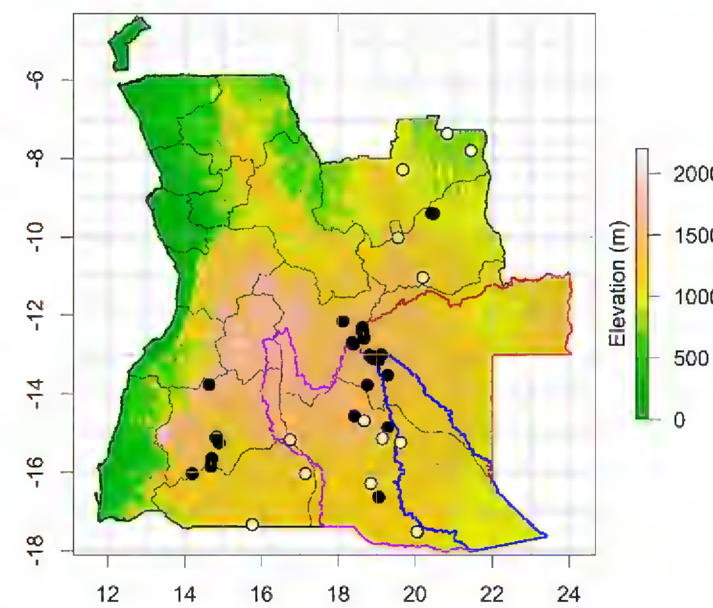


Map 19. Distribution of *Ichnotropis bivittata* in Angola.

Fig. 20. Adult male *Ichnotropis capensis* from Lungwebungu River camp. *Photo by Werner Conradie*.

Fig. 21. Adult female *Ichnotropis capensis* from Sombanana village. *Photo by Werner Conradie*.

Fig. 22. Juvenile *Ichnotropis capensis* (iNaturalist 12228725) from east of Cuemba. *Photo by Alex Rebelo*.



Map 20. Distribution of *Ichnotropis capensis* in Angola.

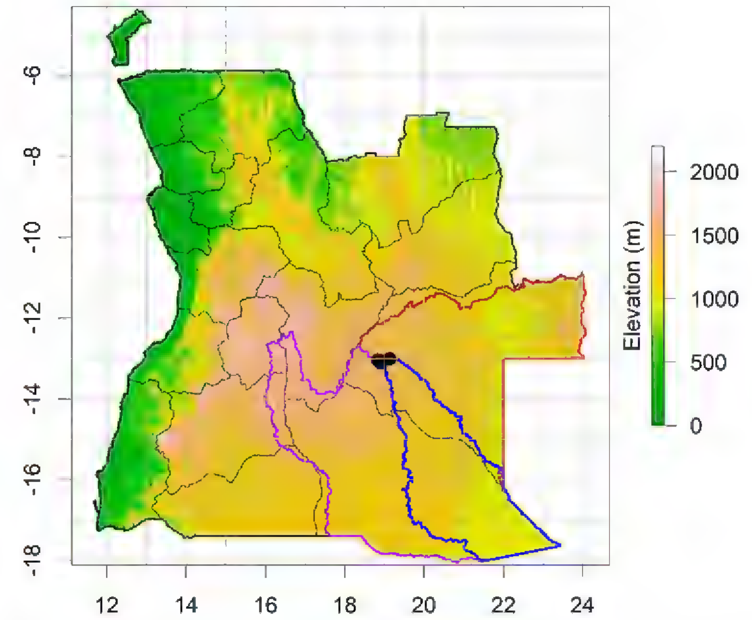
(2019) found that material from the type locality of *I. b. pallida* (KTH09-075 and AMB 10722) shows very little genetic difference from typical *I. bivittata* (JVV 2970 and CAS 258409), and thus should remain in the synonymy of the latter until more material becomes available for a detailed phylogenetic study.

Ichnotropis capensis (Smith, 1838)
Cape Rough-scaled Lizard (Figs. 20–22, Map 20)
Material (66 specimens): PEM R23274–8, Cuanavale River source, -13.0933° 18.89396°, 1,367 m asl; PEM R23253–4, Cacundu falls, -13.7739° 18.7552°, 1,281 m asl; PEM R23298, grasslands W of Cuanavale to Samanunga village, -13.07508° 18.88481°, 1,366 m asl; PEM R23326–8, INBAC: (no number); Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23351–3, Kulua River source, 6 km SE of Cuito River source, -12.736749° 18.3931022°, 1,446 m asl; PEM R23370, INBAC: (no number), Cuanavale River source, -14.85472° 19.28639°, 1,203 m asl; PEM R23409–10, Lungwebungu River camp bridge crossing, -12.58346° 18.66598°, 1,304 m asl; PEM R23414–9, Cuando River source, -13.00345° 19.12751°, 1,343 m asl; PEM R23440, INBAC: (no number x2), Cuando River source trap 1, -13.00393° 19.12808°, 1,351 m asl; PEM R23453, INBAC: WC-4584 (plus 1 additional specimen), Quembo River trap 4, -13.13586° 19.04709°, 1,368 m asl; PEM R23489, Quembo River trap 2, -13.13544° 19.04397°, 1,375 m asl; PEM R23493–5, Cuanavale River source lake camp side, -13.09442° 18.89372°, 1,396 m asl; PEM R23502, Sombanana village, -12.31082° 18.62392°, 1,403 m asl; PEM R23505–7, source lake north of Lungwebungu River crossing, -12.41024° 18.63483°, 1,414 m asl; PEM R23508–9, amphitheatre at Cuanavale River source, -13.05048° 18.89623°, 1,415 m asl; PEM R23521–2, grassland drive west of Cuanavale River source, -13.01347° 18.81669°, 1,538 m asl; PEM R23531, Sombanana village, Dala River, -12.3071° 18.6235°, 1,407 m asl; PEM R23539, Longa River, -14.55956° 18.41419°, 1,321 m asl; PEM R23546–8, Quembo River source camp, -13.14557° 19.04571°, 1,423 m asl; PEM R23977, Lungwebungu River near trap 2, ad hoc, -12.58200° 18.66562°, 1,208 m asl; PEM R23986, Lungwebungu River trap 1, -12.580126° 18.667396°, 1,298 m asl; PEM R23996–7, INBAC: WC-4544 (plus 2 additional specimens), Lake Tchanssengwe, -12.41402° 18.64418°, 1,393 m asl; PEM R27393, INBAC: WC-6796, Cuanavale River source lake, -13.09052° 18.89394°, 1,357 m asl; PEM R27394–401, INBAC: WC-6796, Quembo River bridge camp, -13.52745° 19.2806°, 1,241 m asl. **Description:** 35–46 (40) midbody scale rows; 8–10 (9) longitudinal

Fig. 23. Adult male *Ichnotropis* cf. *grandiceps* from Cuando River source. *Photo by Werner Conradie*.

Fig. 24. Adult female *Ichnotropis* cf. *grandiceps* from grasslands west of Cuanavale River source to Samanunga village. *Photo by Werner Conradie*.

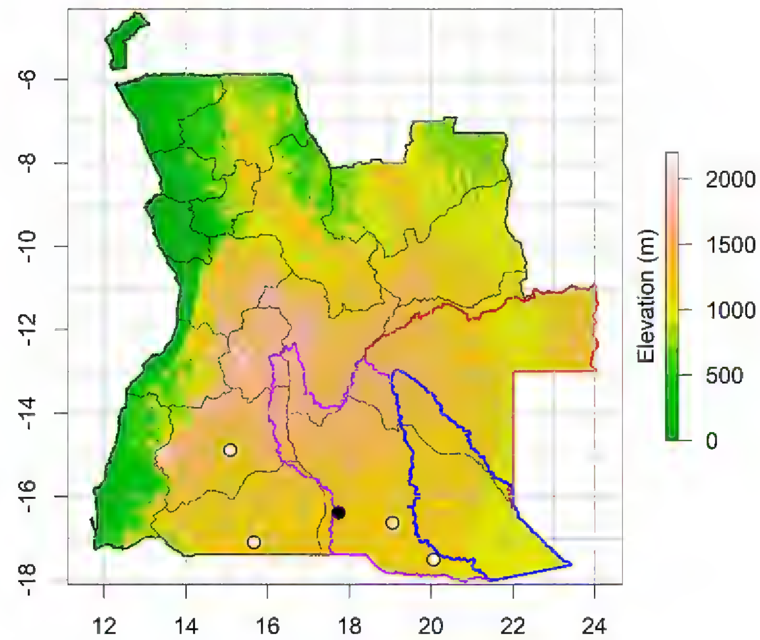
Fig. 25. Juvenile *Ichnotropis* cf. *grandiceps* (PEM R23300) from Cuanavale River source. *Photo by Werner Conradie*.



Map 21. Distribution of *Ichnotropis* cf. *grandiceps* in Angola.

rows of enlarged ventral plates; 26–31 (27) transverse ventral scale rows; 4–5 supralabials; 6–7 infralabials; 4/4 supraciliaries; 19–26 (22) subdigital lamellae under 4th toe; 9–13 (10) femoral pores per thigh. Largest female: 63.1 + 117.0 mm (PEM R23531); largest male: 67.7 + 160.0 mm (PEM R23410, new maximum size record). **Habitat and natural history notes:** In February 2016 and April 2018, only juveniles and subadult specimens were observed, while in October 2016 and November 2019 only adult specimens were observed. **Comment:** Based on general coloration and morphology, we assign these specimens to the widespread *I. capensis.* The large series of material (adults, subadults, and juveniles) allowed us to assess the color variability within this species, and in doing so we could confirm that previous material assigned to *Ichnotropis* sp. by Conradie et al. (2016) and *I. b. pallida* by Butler et al. (2019) and Bandeira (2019) is referrable to subadult *I. capensis.* The status of *I. c. overlaeti* remains unresolved, although Marques et al. (2018) suggest that it might be a valid species based on its geographical separation from the nominotypical form that occurs further south. These new records and unpublished PEM records from Saurimo in Lunda Sul Province breach the distributional gap, potentially forming a link between the southern and northwestern Zambian and DRC records (Haagner et al. 2000; Pietersen et al. 2021).

Ichnotropis cf. *grandiceps* Broadley, 1967
Caprivi Rough-scaled Lizard (Figs. 23–25, Map 21)
Material (17 specimens): PEM R23279–80; INBAC (no number), Cuanavale River source, -13.0933° 18.89396°, 1,367 m asl; PEM R23299–300, Grassland W of Cuanavale River to Samanunga village, -13.07508° 18.88481°, 1,366 m asl; PEM R23303–9, 4 km upstream from Cuanavale River source, -13.05084° 18.89726°, 1,380 m asl; PEM R23361–2, drive to Cuanavale River camp from Samanunga village, -13.03803° 18.82977°, 1,605 m asl; PEM R23420–1, Cuando River source, -13.00345° 19.12751°, 1,343 m asl; PEM R23482, Cuando River source Trap 4, -13.00164° 19.1296°, 1,372 m asl. **Description:** 41–49 (44) midbody scale rows; 9–10 (10) longitudinal ventral scale rows; 30–37 (34) transverse ventral scale rows; 4–5 supralabials; 6–7 infralabials; 5–6 supraciliaries; 19–26 (22) subdigital lamellae under 4th toe; 10–13 (12) femoral pores per thigh. Largest female: 78.2 + 126.0 mm (PEM R23362); largest male: 73.5 + 95t mm (PEM R23420, longest tail measured 117 mm [2x SVL]). **Habitat and natural history notes:** Juveniles were only observed in February 2016 on sandy areas around the source of the Cuanavale River, while two adults were found on the elevated grassland ridges. In October



Map 22. Distribution of *Meroles squamulosus* in Angola.

2016, only adult specimens were found in sympatry with adult *I. capensis*. **Comment:** Described from the Zambezi Region in northeastern Namibia based on only three specimens (Broadley 1967), and further known only from four additional specimens collected from northeastern Namibia (Haacke 1970) and one specimen from western Zambia (Pietersen et al. 2017). The newly collected material conforms in part (broad head, large overall size, dorsal coloration, and higher midbody scale counts) with the original description. These therefore represent the first records from Angola and the largest series of specimens for this species ever collected. The species displays a substantial amount of ontogenetic variation (coloration and size), which originally led to the belief that the juveniles and adults of *I. grandiceps* represented separate species (W. Conradie, pers. obs.). Since this is the first genetic material available for this species, a phylogenetic study is underway (W. Conradie, in prep.).

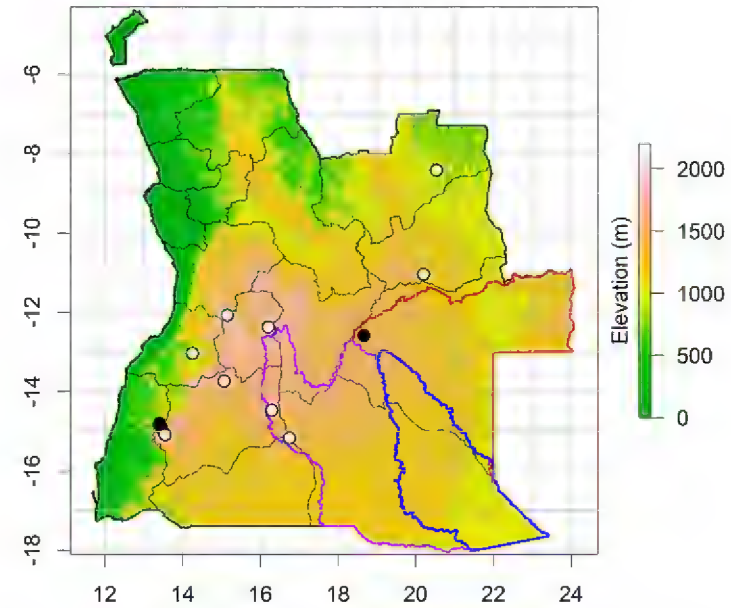
Meroles squamulosus (Peters, 1854)
Common Rough-scaled Lizard (Map 22)
Material (1 specimen): PEM R24291, EN140 road between Caiundo and Katwitwi, -16.38169° 17.7337°, 1,143 m asl. **Description:** 53 midbody scale rows; 8 longitudinal and 36 transverse ventral scale rows; 7/7 supralabials; 7/7 infralabials; 4/4 supraciliaries; 17 subdigital lamellae under 4th toe; 14 femoral pores per thigh. Largest male: 60.8 + 88.0 mm (PEM R24291). **Habitat and natural history notes:** Found active during the day in Zambezian *Baikiaea* woodland. **Comment:** This species is only known from a handful of records in southern Angola (Monard 1937; Conradie et al. 2016), although it is more widespread further south and east (Branch 1998; Pietersen et al. 2021).

Scincidae

Eumecia anchietae Bocage, 1870
Anchieta's Serpentiform Skink (Fig. 26, Map 23)
Material (1 specimen): PEM R23983 (iNaturalist 12410715), Lungwebungu River campsite, ad hoc, -12.58027° 18.66278°, 1,302 m asl. **Description:** Dorsal scales with two keels per scale; tail 1.3 times the SVL; 22 midbody scale rows; 107 transverse ventral scale rows; 3/4 supralabials; 4/4 infralabials; 4 supraciliaries (1st semi-divided); 2 toes on front limbs and 3 on hind limbs. Size (male): 127.0 + 157.0 mm (PEM R23983). **Habitat and natural history notes:** Found dead on road. Stomach contained unidentified grasshopper, caterpillar, and small beetles. **Comment:** Laurent (1964) described *E. a. major* from northern Angola, based on the first supraciliary being fused with the second. Monard (1937) documented the same difference for material from Lunda. The new specimen reported here conforms to the description of *E. a. major* and was collected in close proximity to the material documented by Laurent (1964). The status of this subspecies needs to be determined using phylogenetic analyses.

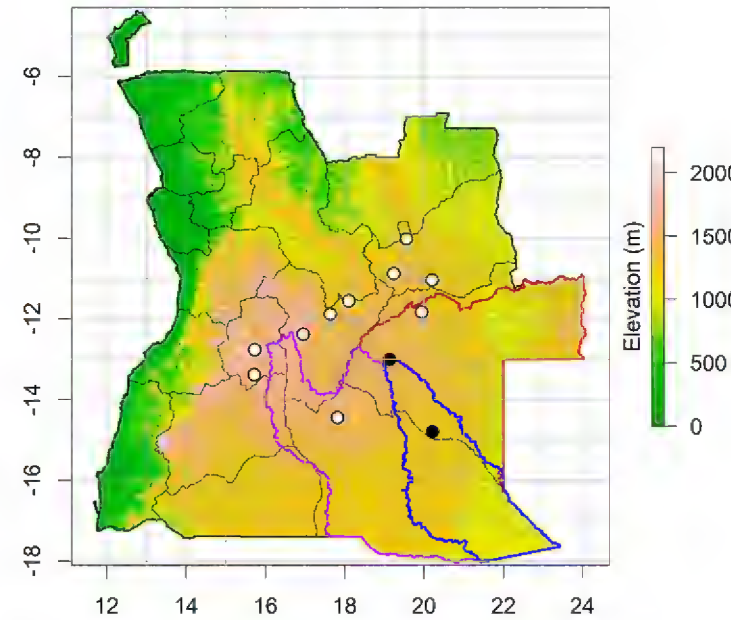
Lubuya ivensii (Bocage, 1879)
Iven's Water Skink (Fig. 27, Map 24)
Material (2 specimens): PEM R23422, Cuando River source, -13.00345° 19.12751°, 1,343 m asl;

Fig. 26. Subadult male *Eumecia anchietae* (PEM R23983) from Lungwebungu River campsite. *Photo by Werner Conradie*.



Map 23. Distribution of *Eumecia anchietae* in Angola.

Fig. 27. Juvenile *Lubuya ivensii* (PEM R23422) from Cuando River source. *Photo by Werner Conradie.*

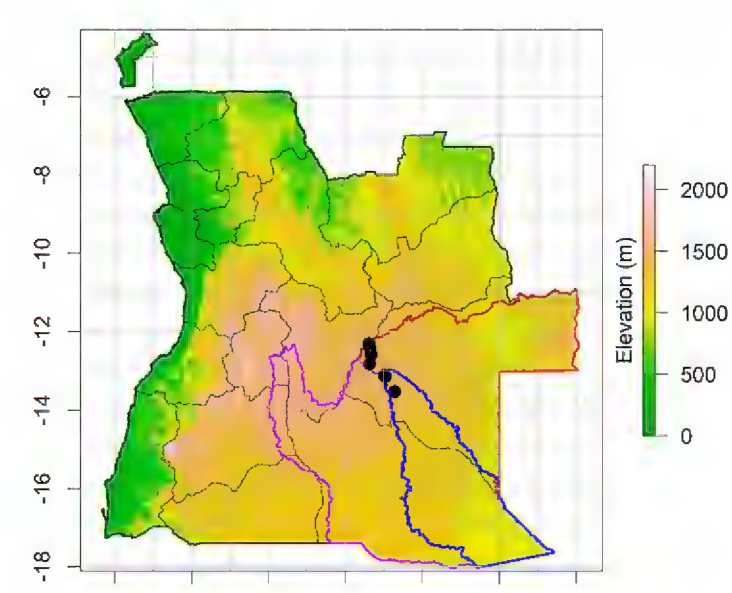


Map 24. Distribution of *Lubuya ivensii* in Angola.

PEM R24276, Cuando River, Camp 19, -14.79365° 20.20482°, 1,121 m asl. **Description:** Dorsal scales with three keels each; tail twice SVL; 29 midbody scale rows; 64–66 transverse ventral scale rows; 62–64 transverse ventral scale rows; 6–7 supralabials; 6 infralabials; 3–4 supraciliaries; 16–19 subdigital lamellae under 4th toe. Largest specimen: 113.0 + 216.0 mm (PEM R24276). **Habitat and natural history notes:** One of the specimens was caught basking on top of dense grass within a grassy wetland. **Comment:** Monard (1937) reported that the material from northeastern Angola has an extra lateral white line, but took no taxonomic action. Subsequently, Laurent (1964) described northeastern material as *Mabuya ivensi septemlineata.* Branch and Haagner (1993), while reporting on a large collection of specimens from northwestern Zambia and adjacent DRC, found no evidence to support the continued recognition of *M. i. septemlineata*. The two new records reported here and the record in Conradie et al. (2016) represent the most southern records of this species and the first from the Okavango and Cuando River basins.

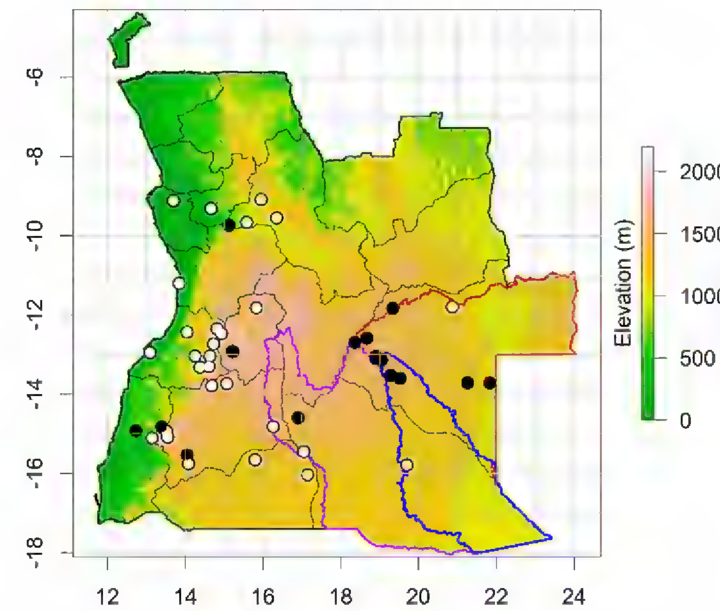
Panaspis sp.
Snake-eyed Skink (Fig. 28, Map 25)
Material (14 specimens): PEM R23317, Protea stop en route to Cuito River source, -12.3004° 18.6207°, 1,425 m asl; PEM R23347, road from Cuanavale River to Cuito River sources, -12.81739° 18.63236°, 1,446 m asl; PEM R23411, Lungwebungu River camp bridge crossing, -12.58346° 18.66598°, 1,304 m asl; PEM R23469, Quembo River source, trap 1, -13.13592° 19.04417°, 1,369 m asl; PEM R23524, Quembo River source, -13.11264° 19.01789°, 1,539 m asl; PEM R23980, Lungwebungu River trap 3, -12.58056° 18.66419°, 1,302 m asl; PEM R23998 (iNaturalist 12261402), Lake Tchanssengwe, -12.41402° 18.64418°, 1,393 m asl; PEM R27407, Quembo River bridge camp, -13.527455° 19.2806°, 1,241 m asl; PEM R27403–6, INBAC: WC-6984, lower Quembo River bridge camp trap 2, -13.52816° 19.28067°, 1,240 m asl. **Description:** No white spots on lateral sides of neck; no dorsolateral white stripes; 25–29 (27) midbody scale rows; 55–61 (57) transverse ventral scale rows; 54–61 (58) transverse dorsal scale rows; 4 supralabials; 7 infralabials; 5–6 supraciliaries; 12–14 (13) subdigital lamellae under 4th toe. Largest female: 41.4 + 56.0 mm (PEM R3524); largest male: 39.2 + 56.0 mm (PEM R23411). **Habitat and natural history notes:** Found among leaf litter in closed canopy miombo woodland. **Comment:** The snake-eyed skinks of Angola were recently reviewed (Ceríaco et al. 2020c) with the recognition of five species occurring in Angola: *P. cabindae*, *P. breviceps*,

Fig. 28. Adult unsexed *Panaspis* sp. (PEM R23347) from en route to the Cuito River source. *Photo by Werner Conradie.*



Map 25. Distribution of *Panaspis* sp. in Angola.

Fig. 29. Adult unsexed *Sepsina angolensis* (PEM R23498) from Cuanavale River source. *Photo by Werner Conradie.*



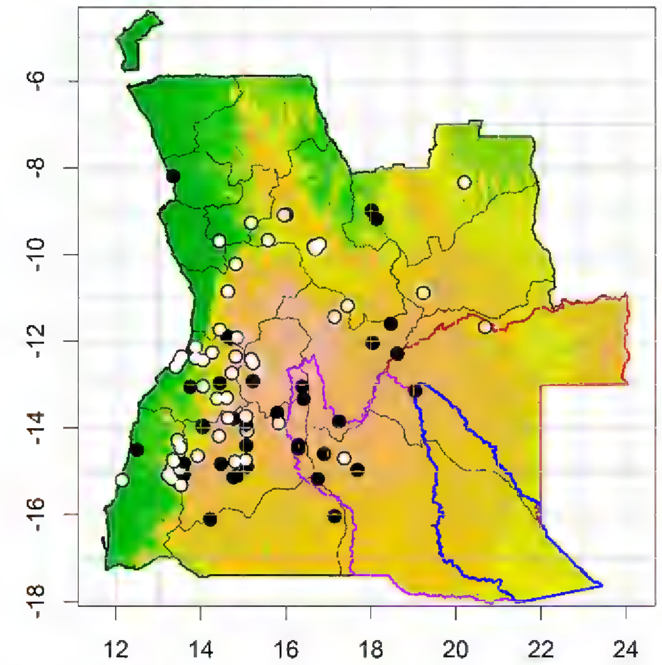
Map 26. Distribution of *Sepsina angolensis* in Angola.

P. wahlbergii, *P. maculicollis,* and the newly described *P. mocamedensis*. Our specimens lack the typical white neck spots diagnostic of the *P. maculicollis* group and the diagnostic black-edged white dorsolateral stripe of the *P. wahlbergii* group. The taxonomic status of this material is pending the outcome of future phylogenetic studies.

Sepsina angolensis (Bocage, 1866)
Angola Reduced-limb Skink (Fig. 29, Map 26)
Material (20 specimens): PEM R23264, Cuchi River gorge, -14.59° 16.90758°, 1,350 m asl; PEM R23316, Cuanavale River, trap 4 active search, -13.05071° 18.89843°, 1,419 m asl; PEM R23332–3, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23460, Quembo River source, trap 5, -13.13586° 19.04709°, 1,368 m asl; PEM R23498–9, INBAC: WC4571, Cuanavale source lake, -13.08934° 18.89485°, 1,396 m asl; PEM R23515, Quembo River source, trap 3, -13.13072° 19.03724°, 1,443 m asl; PEM R23972, Lungwebungu River campsite, ad hoc, -12.58862° 18.66827°, 1,309 m asl; PEM R23978 (iNaturalist 12373403), Lungwebungu River, trap 2, -12.58199° 18.66562°, 1,208 m asl; PEM R27412, Quembo River bridge camp, -13.52816° 19.28067°, 1,240 m asl; PEM R27413,INBAC: WC-6792, Quembo River bridge camp, trap 3, -13.52778° 19.27455°, 1,256 m asl; PEM R27414, Quembo River bridge camp, -13.52745° 19.2806°, 1,241 m asl; PEM R27415, left side tributary (Condinde River) at Cuando River bridge, -13.60076° 19.52675°, 1,219 m asl; PEM R27416, Camp at side tributary (Luandai River) of the Luanguinga River, -13.708854° 21.262343°, 1,116 m asl; PEM R27417, lower Quembo River bridge camp, trap 4, -13.52658° 19.27810°, 1,248 m asl; PEM R27418–9, Luvu River camp, -13.71200° 21.83538°, 1,082 m asl. **Description:** Smooth dorsal scales; 24–25 (24) midbody scale rows; 90–98 (95) transverse ventral scale rows; 89–97 (93) transverse dorsal scale rows; 5–6 supralabials; 6–7 infralabials; 5 supraciliaries; reduced limbs with three clawed toes per limb. Largest female: 84.6 + 56.0 mm (PEM R27413); largest male: 71.0 + 54.0 mm (PEM R23515). **Habitat and natural history notes:** Tracks of these fossorial species can be seen in the early mornings on sandy soil. Most specimens were either caught in traps or by raking through leaf litter. Some specimens were collected under tree logs. **Comment:** This species is known from Angola, Namibia, Zambia, and DRC (Branch 1998; Marques et al. 2018; Pietersen et al. 2021). These records fill the gap within the known distribution in Angola and western Zambia (Broadley 1971; Pietersen et al. 2021).

Trachylepis albopunctata (Bocage, 1867)
White-spotted Variable Skink (Fig. 30, Map 27)
Material (15 specimens): PEM R23256–8, south of Menongue en route to Cuebe River, -14.96288° 17.69089°, 1,300 m asl; PEM R23265, INBAC (no number), Cuchi River gorge, -14.59° 16.90758°, 1,350 m asl; PEM R23344–5, 10 km west of Cuemba village, -12.03481° 18.04869°, 1,437 m asl; PEM R23355, Stop 2: road to Cuito River source, -12.2823° 18.6291°, 1,487 m asl; PEM R23379, Kuvango River hydro plant site, -14.38775° 16.29365°, 1,429 m asl; PEM R23389, INBAC: WC-5207, Cubango River campsite 2 near mission, -13.32887° 16.41167°, 1,520 m asl; PEM R23390, Cubango River, campsite 1 below rapids, west of Fundo village, -13.04483° 16.3752°, 1,557 m asl; PEM R23479, Quembo River source trap 4, -13.13586° 19.04709°, 1,369 m asl; PEM R23543, EN140 North of Menongue, -13.84775° 17.25308°, 1,503 m asl. **Description:** Dorsal scales with three keels each; 30–35 (33) midbody scale rows; 44–47 (45) transverse ventral scale rows; 47–55 (51) transverse dorsal scale rows; 4–6 (5) supralabials; 6–7 (6) infralabials; 4–7 (5) supraciliaries; 19–21 (20) subdigital lamellae under 4th toe. Largest specimen: 55.6 + 92.0 mm (PEM R23265). **Habitat and natural history notes:** Diurnal species found active in miombo woodland. **Comment:** Part of the larger *Trachylepis varia* group (Weinell and Bauer 2018; Weinell et al. 2019). Two species of this group occur in Angola: *T. damarana*, known only from southeastern Angola, and *T. albopunctata*, from the central and coastal regions of Angola. The two species

Fig. 30. Adult unsexed *Trachylepis albopunctata* (PEM R23256) from south of Menongue. *Photo by Werner Conradie.*

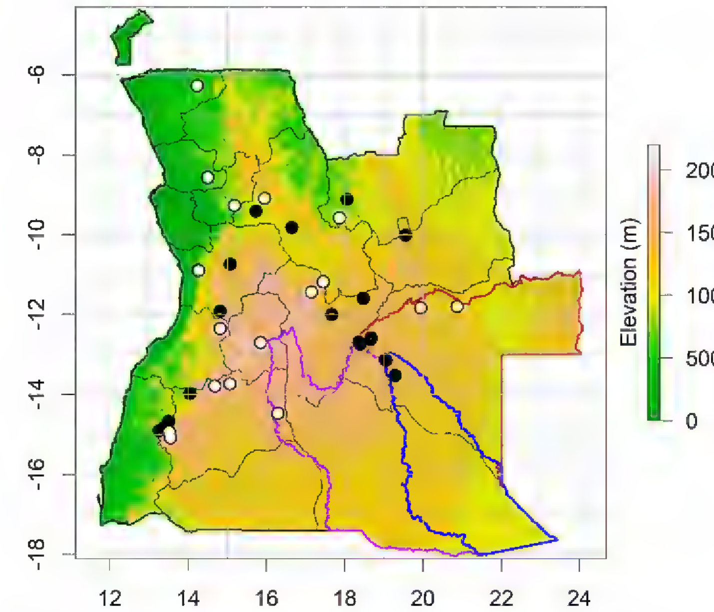


Map 27. Distribution of *Trachylepis albopunctata* in Angola.

can be separated by head scalation and coloration. In *T. albopunctata,* the parietals are mostly in contact anterior of the interparietal (13 out of 19 specimens examined), mostly five supralabials (average 4.6, $n = 22$) that are dark-edged anteriorly, and a mostly uniform dark brown dorsum with less white speckling compared to *T. damarana*.

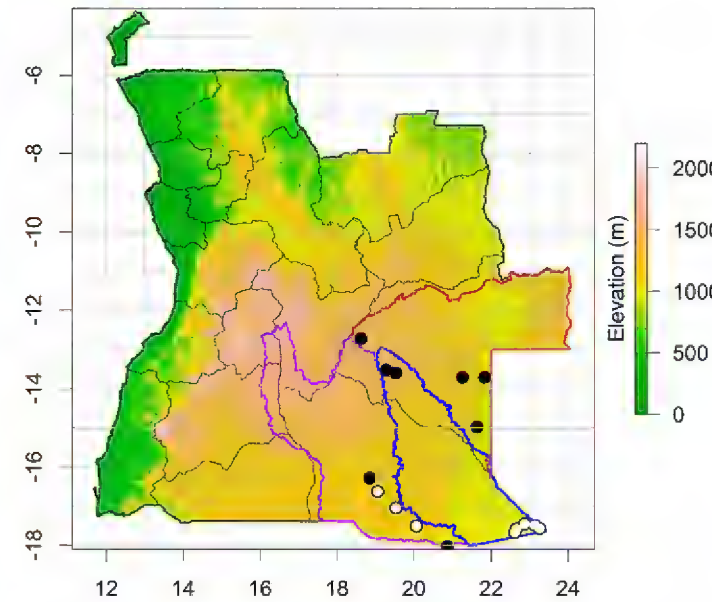
Trachylepis bayonii (Bocage, 1872)
Bayão's Skink (Fig. 31, Map 28)
Material (21 specimens): PEM R23336–8, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23354, Kulua River source lake, 6 km SE of Cuito River source, -12.736749° 18.3931022°, 1,446 m asl; PEM R23378, Kwanza River bridge, -11.99348° 17.66965°, 1,273 m asl; PEM R23477, Quembo River trap 2, -13.13544° 19.04397°, 1,369 m asl; PEM R23478, Quembo River trap 3, -13.13072° 19.03724°, 1,369 m asl; PEM R23501, Quembo River source lake, -13.14104° 19.05426°, 1,399 m asl; PEM R23514, Cuito River source lake, -12.68866° 18.36025°, 1,426 m asl; PEM R23516, Kulua River source, -12.73723° 18.3934°, 1,444 m asl; PEM R23553–5, INBAC: WC-4674, Quembo River source camp, -13.14104° 19.05426°, 1,371 m asl; PEM R23971 (iNaturalist 12347684), Rio Comba, -12.62442° 18.65159°, 1,299 m asl; PEM R23987, Lungwebungu River trap 1, -12.58012° 18.66740°, 1,298 m asl; PEM R27420, Lungwebungu River camp, at bridge, -12.58391° 18.66545°, 1,295 m asl; PEM R27421, Lungwebungu River camp, -12.58439° 18.66748°, 1,297 m asl; PEM R27422, Quembo River bridge camp, trap 1, -13.52801° 19.28147°, 1,236 m asl; PEM R27423–4, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.284866°, 1,248 m asl. **Description**: Dorsal scales with five keels each; scales under toes spinose; 30–35 (32) midbody scale rows; 45–56 (52) transverse ventral scale rows; 40–53 (49) transverse dorsal scale rows; 4–6 supralabials; 6–8 infralabials; 3–4 supraciliaries; 15–17 (16) subdigital lamellae under 4th toe. Largest specimen: 76.2 + 152 mm (PEM R27424). **Habitat and natural history notes:** Lateral sides of body and tail orange in breeding males. **Comment:** Two subspecies are currently recognized: *T. b. bayonii* and *T. b. huilensis*. Weinell et al. (2019) showed that *T. b. huilensis* requires full species recognition. Our new material is tentatively assigned to *T. b. bayonii*, based on distribution and unpublished barcoding results (W. Conradie, unpub. data).

Fig. 31. Adult unsexed *Trachylepis bayonii* from Cuito River source. *Photo by Werner Conradie.*



Map 28. Distribution of *Trachylepis bayonii* in Angola.

Fig. 32. Adult male *Trachylepis damarana* (PEM R27434) from Quembo River bridge camp. *Photo by Chad Keates.*

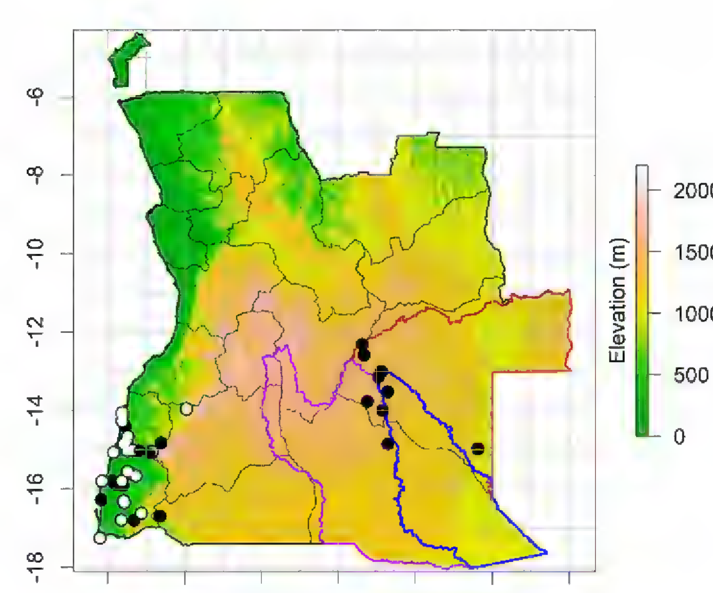


Map 29. Distribution of *Trachylepis damarana* in Angola.

Trachylepis damarana (Peters, 1870)
Damara Variable Skink (Fig. 32, Map 29)
Material (14 specimens): PEM R23266, en route to Cuanavale River source, -12.72368° 18.6228°, 1,355 m asl; PEM R27425–6, PEM R27430, camp at side tributary (Luandai River) of the Luanguinga River, -13.708854° 21.262343°, 1,116 m asl; PEM R27427, R27431, Lake Hundo, -14.974308° 21.629657°, 1,100 m asl; PEM R27428–9, R27432–3, INBAC: WC-6769, Quembo River bridge camp, -13.527455° 19.2806°, 1,241 m asl; PEM R27434, PEM R27436, Quembo River bridge camp, trap 3, -13.527782° 19.274545°, 1,256 m asl; PEM R27435, left side tributary (Condinde River) at Cuando River bridge, -13.60076° 19.52675°, 1,219 m asl; PEM R27437, Luvu River camp, -13.712001° 21.835381°, 1,082 m asl. **Description:** Dorsal scales with three keels each; 30–35 (33) midbody scale rows; 40–46 (43) transverse ventral scale rows; 50–59 (53) transverse dorsal scale rows; 4–5 (4) supralabials; 6–7 (6) infralabials; 4–6 (5) supraciliaries; 20–23 (22) subdigital lamellae under 4th toe. Largest specimen: 59.6 + 0t mm (PEM R27425, longest tail 89.8 mm [1.7 x SVL]). **Habitat and natural history notes:** Lateral sides of body and tail orange in breeding males (Fig. 32). All specimens were found in degraded/ secondary miombo woodland. **Comment:** See *T. albopunctata* species account for details on taxonomy and identification.

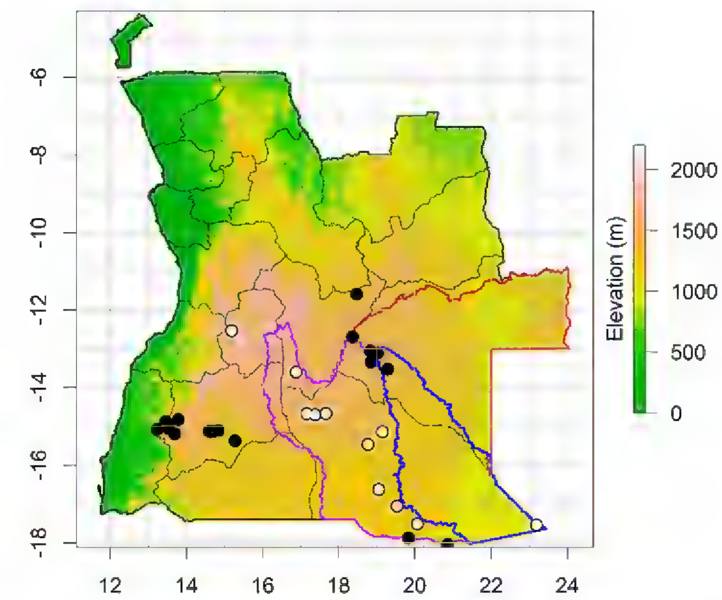
Trachylepis cf. *punctulata* (Bocage, 1872)
Speckled Sand Skink (Fig. 33, Map 30)
Material (18 specimens): PEM R23255, Cacundu falls, -13.7739° 18.7552°, 1,281 m asl; PEM R23371, Cuanavale River source, -14.85472° 19.28639°; PEM R23372, Cuanavale River, -13.99475° 19.14919°; PEM R23425–6, Cuando River source, -13.00345° 19.12751°, 1,343 m asl; PEM R23461–2, Quembo River, trap 4, -13.13586° 19.04709°, 1,368 m asl; PEM R23504, Sombanana village river, -12.3071° 18.6235°, 1,408 m asl; PEM R23550–2, Quembo River source camp, -13.14557° 19.04571°; PEM R23981–2, Lungwebungu River trap 3, -12.58056° 18.66419°, 1,302 m asl; PEM R27438–40, WC-6769, Quembo River bridge camp, -13.52746° 19.28060°, 1,241 m asl; WC-6942, Lake Hundo, -14.974308° 21.629657°, 1,100 m asl. **Description:** Dorsal scales with five keels each; scales under toes spinose; 31–35 (33) midbody scale rows; 45–55 (51) transverse ventral scale rows; 40–50 (45) transverse dorsal scale rows; 5–6 supralabials; 6 infralabials; 4–5 supraciliaries; 16–22 (19) subdigital lamellae under 4th toe. Largest specimen: 46.0 + 45 mm (PEM R 23255). **Habitat and natural history notes:** A small skink that

Fig. 33. Adult unsexed *Trachylepis* cf. *punctulata* from Quembo River source. *Photo by Werner Conradie.*



Map 30. Distribution of *Trachylepis punctulata* in Angola.

Fig. 34. Adult female *Trachylepis* cf. *spilogaster* (PEM R23334) from Cuito River source. *Photo by Werner Conradie.*



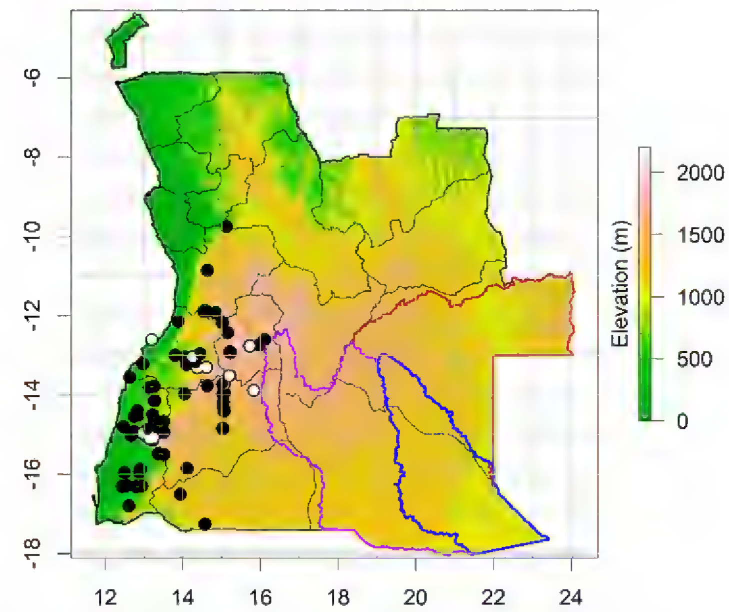
Map 31. Distribution of *Trachylepis* cf. *spilogaster* in Angola.

was often found moving around on the sandier regions, in close proximity to water sources. **Comment:** Most of the Angolan distribution is centred around the arid south-western regions of the country (Marques et al. 2018). Our records are the first from eastern Angola, forming a link with the records from western Zambia and the Zambezi Region of Namibia (Broadley 1971, 1975; Pietersen et al. 2017, 2021). The taxonomic status of this Kalahari Basin population requires further investigation.

Trachylepis cf. *spilogaster* (Peters, 1882)
Kalahari Tree Skink (Fig. 34, Map 31)
Material (7 specimens): PEM R23334–5, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23528, Quembo River source, -13.10699° 19.01785°, 1,545 m asl; PEM R23358–60, DOR en route to village, -13.05967° 18.83239°, 1,567 m asl; PEM R27441, DOR en route between Cuanavale River source and Tempué, -13.33954° 18.85122°, 1,386 m asl; INBAC: WC-6813, Quembo River, walk back from small waterfall, -13.52988° 19.28340°, 1,242 m asl. **Description:** Dorsal scales with five keels each; scales under toes spinose; 35–38 (37) midbody scale rows; 54–59 (57) transverse ventral scale rows; 47–48 (48) transverse dorsal scale rows; 5–6 supralabials; 6 infralabials; 4–6 supraciliaries; 19–20 (20) subdigital lamellae under 4th toe. Largest specimen: 81.4 + 125 mm (PEM R23334). **Habitat and natural history notes:** This species was often observed on the ground at the base of trees but quickly ascended the tree trunks in miombo woodland when disturbed. **Comment:** The status of *Trachylepis* cf. *spilogaster* is discussed by Conradie et al. (2016). Broadley (2000) reported that specimens from northwestern Botswana do not have the characteristic ventral black markings. The new material from the source lakes and material reported by Conradie et al. (2016) either lack ventral markings, or have markings restricted to the gular region. The taxonomic status of this population is currently under review (L. M. P. Ceríaco et al., pers. comm.).

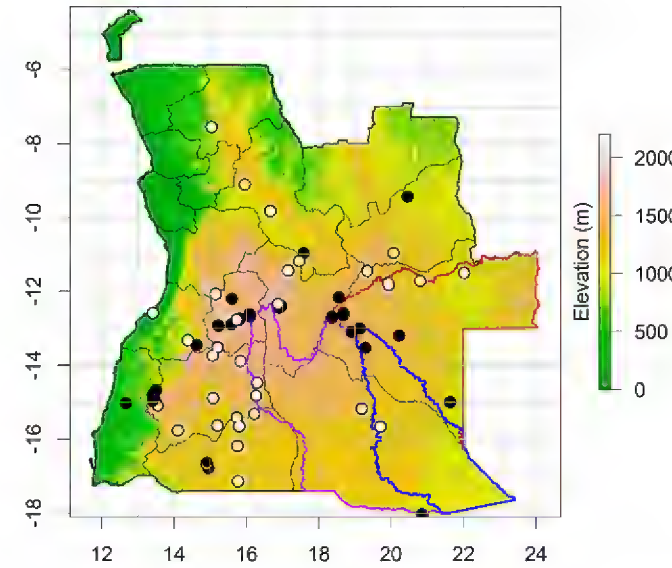
Trachylepis sulcata ansorgii (Boulenger, 1907)
Western Rock Skink (Fig. 35, Map 32)
Material (1 specimen): PEM R23368, en route to Cuito, east of Huambo, -12.73615° 15.97442°, 1,777 m asl. **Description:** Dorsal scales with five keels each; scales under toes smooth; 39 midbody scale rows; 53 transverse ventral scale rows; 49 transverse dorsal scale rows; 5/5 supralabials; 7/7 infralabials; 5/5 supraciliaries; 23 subdigital lamellae under 4th toe. Size: 80.6 + 0t mm. **Habitat and natural history notes:** Rupicolous skink

Fig. 35. Adult female *Trachylepis sulcata ansorgii* (PEM R23368) from en route between Huambo and Cuito. *Photo by Luke Verburgt.*



Map 32. Distribution of *Trachylepis sulcata* in Angola.

Fig. 36. Adult male *Trachylepis wahlbergii* from Cuito town. *Photo by Werner Conradie*.

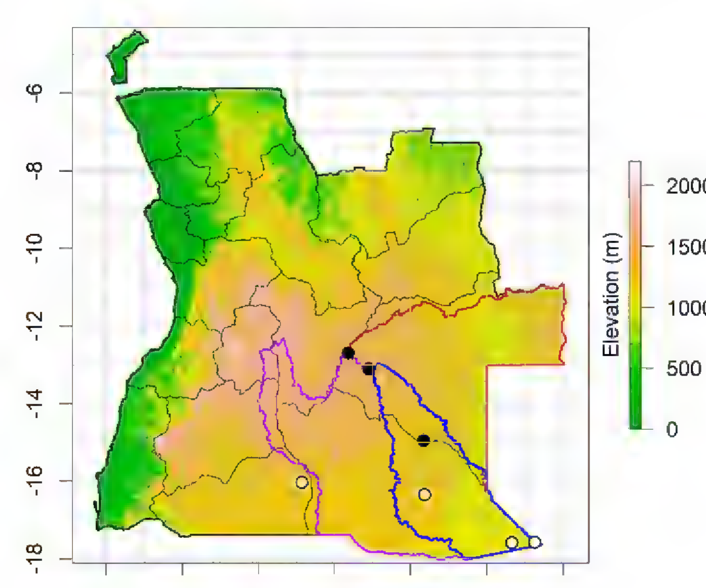


Map 33. Distribution of *Trachylepis wahlbergii* in Angola.

found in sympatry with *Agama planiceps* and *Afroedura wulfhaackei*. **Comment:** Both Butler et al. (2019) and Weinell et al. (2019) showed that *T. s. ansorgii* deserves full species recognition. As this species group is still under taxonomic revision, we mapped it at the species level. Not collected within the core study area, but this record contributes to the overall distribution of this species and the region and this species is expected to occur along the western edge of the study area.

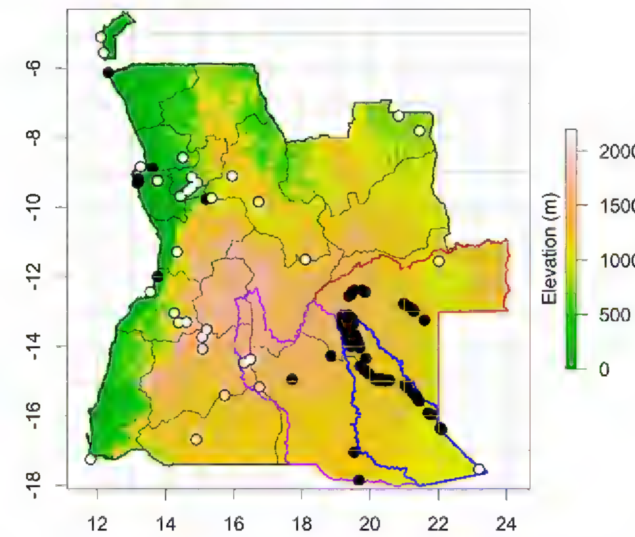
Trachylepis wahlbergii (Peters, 1869)
Wahlberg's Striped Skink (Fig. 36, Map 33)
Material (33 specimens): PEM R23259, en route to Cuanavale River source, -12.63683° 18.65984°, 1,316 m asl; PEM R23289–95, Cuanavale River source, -13.0933° 18.89396°, 1,356 m asl; PEM R23339–41, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23363–6, HALO Cuito, -12.39584° 16.96067°, 1,700 m asl; PEM R23376, outlet of Cuito River source lake, -12.70453° 18.35445°, 1,429 m asl; PEM R23393, Huambo HALO training camp, -12.73726° 15.81828°, 1,667 m asl; PEM R23401, INBAC: WC-5181, Cubango River source site, -12.66051° 16.08998°, 1,777 m asl; PEM R23412, Lungwebungu River camp bridge crossing, -12.58346° 18.66598°, 1,304 m asl; PEM R23427, INBAC (2 x no number), Cuando River source, -13.00345° 19.12751°, 1,343 m asl; PEM R23484–5, INBAC: WC-4776, Cuando River source trap 4, -13.00164° 19.1296°, 1,372 m asl; PEM R23513, Cuito River source lake, -12.68866° 18.36025°, 1,426 m asl; PEM R23559, Munhango village, -12.16067° 18.55042°, 1,428 m asl; PEM R27442, Quembo River bridge camp, -13.527455° 19.2806°, 1,241 m asl; PEM R27443, INBAC (no number), Luio River camp floodplains, -13.197108° 20.221937°, 1,181 m asl; PEM R27444, INBAC: WC-6919, Lake Hundo, trap 1, -14.99158° 21.63096°, 1,100 m asl. **Description:** Dorsal scales with 3–5 keels each; 38–42 (38) midbody scale rows; 51–63 (58) transverse ventral scale rows; 44–52 (49) transverse dorsal scale rows; 5–6 supralabials; 5–8 infralabials; 4–7 supraciliaries; 18–22 (19) subdigital lamellae under 4th toe. Largest female: 88.2 + 105.0 mm (PEM R23364); largest male 86.0 + 104 mm (PEM R23485). **Habitat and natural history notes:** Specimens were mostly encountered running on sand and retreating to holes when approached. No specimens were encountered on trees. **Comment:** This species has a wide distribution in southern Africa (Branch 1998; Pietersen et al. 2021) and Angola (Marques et al. 2018). The taxonomy of the *Trachylepis striata* species complex, to which this species belongs, is still unresolved and requires further investigation (Weinell et al. 2019; Stephens et al. 2021).

Fig. 37. Adult unsexed *Typhlacontias rohani* (PEM R27445) from Cuanavale River source. *Photo by Werner Conradie*.



Map 34. Distribution of *Typhlacontias rohani* in Angola.

Fig. 38. Adult unsexed *Varanus niloticus* from en route between the Munhango and Cuanavale River sources. *Photo by Werner Conradie*.



Map 35. Distribution of *Varanus niloticus* in Angola.

Typhlacontias rohani Angel, 1923
Rohan's Blind Legless Skink (Fig. 37, Map 34)
Material (5 specimens): PEM R23342, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23497, Cuanavale River source lake, camp side, -13.09442° 18.89372°, 1,396 m asl; PEM R24279, Cuando River, Camp 21, -14.94935° 20.34483°, 1,115 m asl; PEM R27445, Cuanavale River source lake, -13.090523° 18.89394°, 1,357 m asl; PEM R27446, en route from Cuando River to Cangamba. **Description:** Dorsal scales smooth; 18 midbody scale rows; 117–129 (123) transverse dorsal scale rows; 4 supralabials; 4 infralabials; 2 supraciliaries. Largest specimen: 76 + 39.8 mm (PEM R27445). **Habitat and natural history notes:** All specimens were found while raking through leaf litter in sandy soil. **Comments:** This fossorial legless skink is known from southeastern Angola, northeastern Namibia, western Zimbabwe, northern Botswana, and western Zambia (Haacke 1997; Marques et al. 2018; Pietersen et al. 2021). Although described from southeastern Angola (Angel 1923), very few records exist for the country (Monard 1937; Conradie et al. 2016). These new records are the northernmost for Angola. Most of the genus is restricted to the western coastal regions of Namibia and Angola, with only two species occurring in the Kalahari Basin, i.e., *T. rohani* and *T. gracillis*. The former is widespread while the latter is restricted to western Zambia. The two species occur in sympatry at Kalabo in western Zambia (Haacke 1997). Future studies should utilize an integrative systematic approach to elucidate the species boundaries and taxonomic structuring within the whole genus.

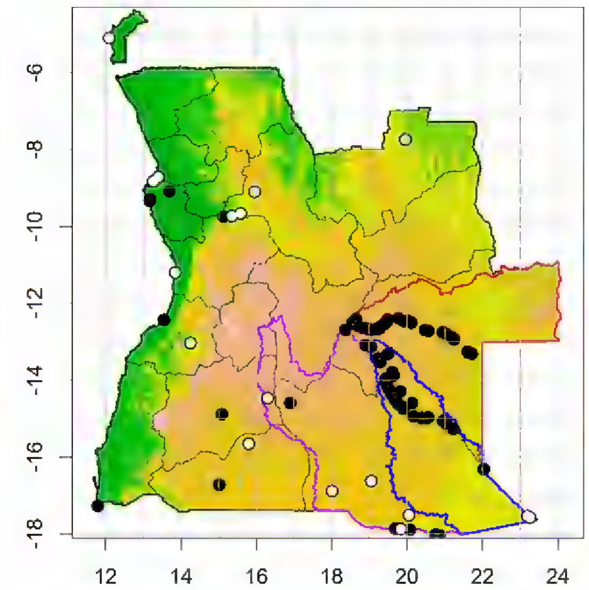
Varanidae

Varanus niloticus (Linnaeus, 1766)
Water Monitor (Fig. 38, Map 35)
Observations: Cuando River -13.09320° 19.36016°, -13.10063° 19.37254°, -13.12122° 19.39664°, -13.17326° 19.42046°, -13.18493° 19.43374°, -13.19005° 19.44007°, -13.19016° 19.44147°, -13.20209° 19.46860°, -13.21743° 19.45877°, -13.31917° 19.49327°, -13.32957° 19.49497°, -13.35510° 19.50343°, -13.35558° 19.50442°, -13.67297° 19.56172°, -13.79270° 19.61024°, -13.85453° 19.629620°, -13.90348° 19.65057°, -13.92381° 19.65753°, -14.03595° 19.69015°, -14.27281° 18.85794° (iNaturalist 1727927), -14.346620° 19.87581°, -14.92236° 20.31874°; Quembo River -13.17842° 19.13734°, -13.25178° 19.17143°, -13.25356° 19.17294°, -13.29163° 19.18123°, -13.33984° 19.20500°, -13.43206° 19.23945°, -13.48539° 19.24675°, -13.56702° 19.305067°, -13.56871° 19.30585°, -13.67061° 19.35595°, -13.67866° 19.35836°, -13.77110° 19.37386°, -13.79160° 19.38176°, -13.80572° 19.38648°, -13.81202° 19.38591°, -13.88262° 19.39604°, -13.93431° 19.42397°, -13.93599° 19.42577°, -13.99462° 19.43543°, -14.55758° 19.70635°, -14.67219° 19.83275°, -14.68235° 19.84010°, -14.68799° 19.85021°, -14.74537° 19.90861°, -14.76761° 19.93762°, -14.77509° 19.95381°, -14.92917° 20.15534°, -14.95729° 20.21396°, -14.95792° 20.36728°, -14.96685° 20.29766°, -14.96740° 20.46661°, -14.97001° 20.56494°, -14.97947° 20.23928°, -14.97965° 20.43558°, -14.98357° 20.45164°, -15.12585° 21.03947°, -15.18248° 21.08478°, -15.34301° 21.25209°, -15.42151° 21.34750°, -15.42435° 21.34192°, -15.49507° 21.38893°, -15.53690° 21.40043°, -15.58262° 21.43537°, -15.92187° 21.70659°, -15.96243° 21.79459°, -16.34916° 22.06133°, -16.37759° 22.069423°, -16.38589° 22.08581°, -16.39687° 22.097313°; Lungwebungu River -12.55000° 19.37939°, -12.50378° 19.44091°, -12.43436° 19.47018°, -12.38381° 19.54014°, -12.38389° 19.77781°, -12.40754° 19.80887°, -12.42778° 19.84023°, -12.43711° 19.85936°, -12.77029° 20.98921°, -12.80185° 21.03409°, -12.81192° 21.04544°, -12.85937° 21.14091°, -12.93685° 21.24336°, -12.95462° 21.26790°, -12.98417° 21.28638°, -13.24428° 21.59976°. **Comment:** This species was mostly encountered on the banks of rivers or basking on overhanging fig trees. However, one individual was captured very far from any known water source, presumably during a migration event between water sources.

Crocodylia
Crocodylidae

Crocodylus niloticus Laurenti, 1768
Nile Crocodile (Fig. 39, Map 36)

Fig. 39. Juvenile *Crocodylus niloticus* from Quembo River bridge camp. *Photo by Chad Keates.*



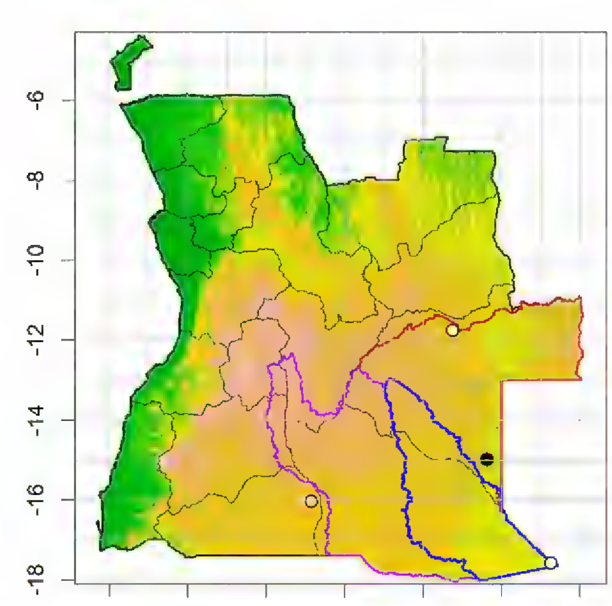
Map 36. Distribution of *Crocodylus niloticus* in Angola.

Observations: Cuito River source lake, -12.68935° 18.36012°; Cuchi River gorge, -14.59000° 16.90758°, 1,350 m asl; Kulua River source, lake 6 km SE of Cuito source, -12.736749° 18.3931022°, 1,446 m asl; Cuanavale River source lake, -13.09052° 18.89394°; Quembo River source lake, -13.13586° 19.04709°; Quembo River bridge site, -13.52801° 19.28147°; Lake Tchanssengwe, -12.41402° 18.64418°, 1,393 m asl; Cuando River -13.32009° 19.49338°, -13.79438° 19.60793°, -13.88734° 19.64641°, -14.29429° 19.81956°, -14.602330° 20.13131°, Quembo River -13.43374° 19.24170°, -13.53046° 19.28822°, -13.96865° 19.42061°, -13.99376° 19.43288°, -14.027810° 19.44206°, -14.09658° 19.46397°, -14.11456° 19.46687°, -14.15561° 19.48322°, -14.15577° 19.48615°, -14.22304° 19.50668°, -14.27701° 19.54167°, -14.34465° 19.57520°, -14.38198° 19.60944°, -14.39925° 19.61876°, -14.41994° 19.63391°, -14.51911° 19.69112°, -14.61351° 19.76039°, -14.67203° 19.83250°, -14.73636° 19.90068°, -14.94193° 20.16986°, -14.96962° 20.55838°, -14.97661° 20.53455°, -14.97668° 20.50791°, -14.97877° 20.38383°, -14.9834° 20.51638°, -15.05622° 20.95461°, -15.12544° 21.03706°, -15.26815° 21.23438°, -16.31355° 22.0369°, -16.31651° 22.0363°; Lungwebungu River -12.51823° 18.54648°, -12.57812° 18.67840°, -12.63833° 18.82899°, -12.64124° 18.86644°, -12.67050° 18.96596°, -12.68586° 19.06160°, -12.66937° 19.17765°, -12.66345° 19.21794°, -12.65688° 19.25919°, -12.60808° 19.29928°, -12.57965° 19.34484°, -12.52636° 19.40970°, -12.45915° 19.47460°, -12.45031° 19.47158°, -12.41964° 19.48228°, -12.38694° 19.77156°, -12.45968° 19.90906°, -12.45414° 20.005371°, -12.45218° 20.01162°, -12.48533° 20.09848°, -12.50573° 20.11481°, -12.70198° 20.47726°, -12.72187° 20.56667°, -12.75665° 20.94848°, -12.78606° 21.02360°, -12.88576° 21.18927°, -12.93852° 21.24419°, -13.25902° 21.61123°, -13.28100° 21.62614°, -13.31189° 21.71873°. **Comment:** No evidence was found that this species was breeding in the upper reaches of the rivers.

Testudines
Pelomedusidae

Pelusios bechuanicus FitzSimons, 1932
Okavango Mud Terrapin (Fig. 40, Map 37)
Material (2 specimens): PEM R27408–9, Lake Hundo, -14.97431° 21.62966°, 1,100 m asl. **Description:** Specimen with large carapace (235 mm; PEM R27409) collected on the edge of a lake and a sub-adult female (123 mm; PEM R27408) collected from the lake itself. Head black with yellow blotches; plastron and carapace uniform black; front limbs black with yellow markings; interlimb skin pale white. **Habitat and natural history notes:** The specimen caught alive was captured with a

Fig. 40. Subadult female *Pelusios bechuanicus* (PEM R27408) from Lake Hundo. *Photo by Werner Conradie.*



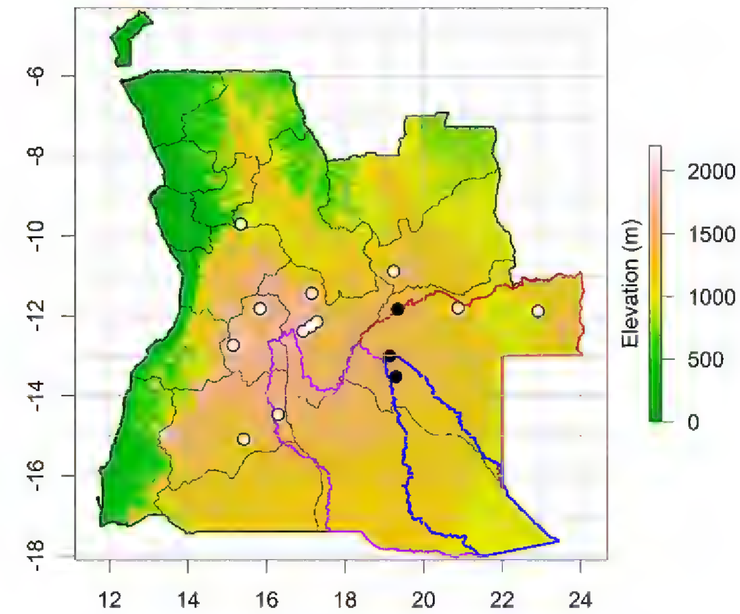
Map 37. Distribution of *Pelusios bechuanicus* in Angola.

Fig. 41. Adult female *Pelusios nanus* (PEM R23423) from Cuando River source. *Photo by Werner Conradie.*

net while collecting fish in the deeper waters of the lake. **Comment:** This is only the 4th record of this species for Angola (see Conradie et al. 2016; Marques et al. 2018). Elsewhere this species is restricted to the Okavango and Zambezi River systems (Pietersen et al. 2021).

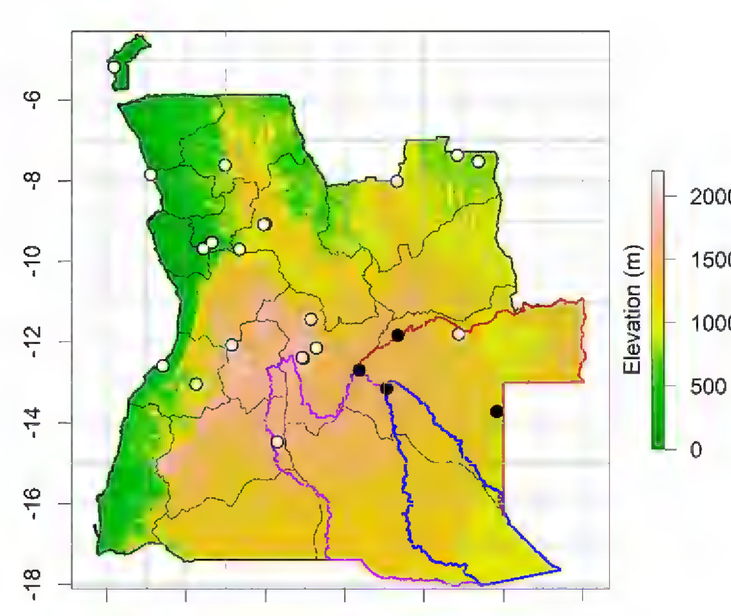
Pelusios nanus Laurent, 1956
African Dwarf Mud Terrapin (Fig. 41, Map 38)
Material (2 specimens): PEM R23423, Cuando River source, -13.00345° 19.12751°, 1,343 m asl; PEM R27410 (shell), Quembo River bridge camp, -13.52745° 19.2806°, 1,241 m asl. **Description:** Carapace lengths 91.6 mm (PEM R27410) and 88.4 mm (PEM R23423), respectively. Carapace very smooth and rounded, uniform dark brown with black edges to scutes; plastron beige with lateral and anterior edges dark brown to black; head brown with yellow vermiculation; limbs dark brown; skin of neck and limbs light yellow. **Habitat and natural history notes:** The live specimen was caught in shallow water covered by grass at the source of the Cuando River. **Comment:** The new records close the distributional gap between the central and eastern Angolan records (Marques et al. 2018) and are the first from the Cuando River basin.

Fig. 42. Subadult female *Pelusios rhodesianus* (PEM R23329) from Cuito River source. *Photo by Werner Conradie.*



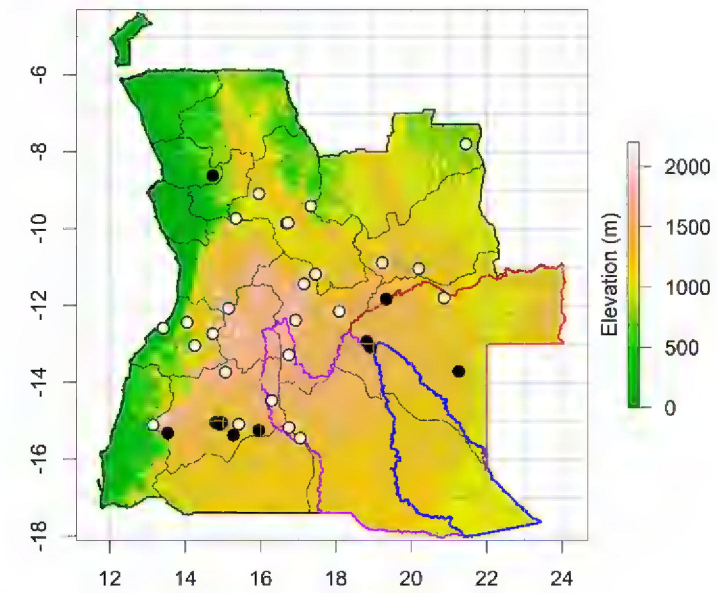
Map 38. Distribution of *Pelusios nanus* in Angola.

Pelusios rhodesianus Hewitt, 1927
Variable Mud Terrapin (Fig. 42, Map 39)
Material (4 specimens): PEM R23329, Cuito River source lake, -12.68935° 18.36012°, 1,435 m asl; PEM R23490 (shell), Quembo River source, -13.13959° 19.04890°, 1,375 m asl; PEM R23562, en route to the Cuando and Quembo confluence; PEM R27411, Luvu River camp, -13.71200° 21.83538°, 1,082 m asl; uncatalogued individual from middle Cubango River. **Description:** Most specimens were juveniles, but one adult carapace measured 177 mm (PEM R23490). The carapace and plastron of the shell were uniform dark brown to black. Juveniles had dark brown carapaces, but the plastrons varied from uniform black to beige with darker centers; head and limbs uniform brown; interlimb skin white to yellowish. The adult carapace was elongate and smooth with a weak vertebral keel anteriorly, while all the juveniles' carapaces were rounded with a pronounced vertebral crest. **Habitat and natural history notes:** Juvenile specimens were caught with a net while collecting fish in the deeper waters of the lake and rivers. **Comment:** The new records fill the gap in the known distribution between central Angola and the Okavango Delta (Rhodin et al. 2021).



Map 39. Distribution of *Pelusios rhodesianus* in Angola.

Fig. 43. Adult female *Kinixys belliana* from Samanunga village. *Photo by Werner Conradie*.



Map 40. Distribution of *Kinixys belliana* in Angola.

Testudinidae

Kinixys belliana Gray, 1831
Bell's Hinge-back Tortoise (Fig. 43, Map 40)
Observations: Camp at side tributary (Luandai River) of the Luanguinga River, -13.70885° 21.26234°, 1,116 m asl; Samanunga village, approx. -12.93169° 18.81458°; between Tempué and Cuanavale, approx. -13.07438° 18.9075°. **Habitat and natural history notes:** All specimens were collected or encountered in miombo woodland. **Comment:** According to the revision of the *Kinixys* genus by Kindler et al. (2012), eastern Angolan material should be assigned to *Kinixys belliana.*

Discussion

The findings of this study contribute to our growing knowledge of the Angolan herpetofauna, increasing the number of documented lizard, chelonian, and crocodile species in the country from 157 to approximately 161. This number is expected to increase even more in the coming years as more remote regions are surveyed and taxonomic revisions that are currently underway are completed. Southeastern Angola has been regarded as one of the most poorly studied regions in Angola (Marques et al. 2018). Due to a series of biodiversity surveys in the region since 2012 (Conradie et al. 2016, 2021; this study) our knowledge of the region has grown, resulting in a more robust understanding of the herpetofaunal diversity of southeastern Angola. However, most of the records originate from the more easily accessible areas, while most of southeastern Angola remains unexplored due to its remoteness and lack of road infrastructure. Consequently, the region is likely to harbor additional species that were not detected during the surveys in this study and will require further explorative surveys in the near future.

At a regional level, the results of this survey raise the number of lizard, chelonian, and crocodile species known from the Angolan Okavango-Cuando River system to 52, an increase of 14 species from a previously compiled checklist for the region (Conradie et al. 2016). When the Zambezi River system is included, the number of species recorded for southeastern Angola increases to 58.

Since a previous compilation of historical records for Angola (Marques et al. 2018), citizen science activity has escalated dramatically, and numerous additional biodiversity expeditions in Angola have increased the number of herpetological records from Angola. This new information has led to an increase of ~60% in the new unique occurrence records for Angola, and allowed us to update the distribution maps for the 40 species documented during this study. Many of these new records fill the gaps between the central Angolan and western Zambian records (e.g., *Chamaeleo dilepis*, *Ichnotropis capensis*, and *Sepsina angolensis*), demonstrating that these species have more continuous distributions than previous data had suggested.

The results of this study confirm the presence of three species that were previously only predicted (Conradie et al. 2016; Marques et al. 2018) to occur in the region (i.e., *Pachydactylus wahlbergii*, *Lygodactylus chobiensis*, and *Ichnotropis* cf. *grandiceps*). Our records of these three species also represent the first confirmed country records. The presence of *Agama armata* from eastern Angola was confirmed with records from Huambo region (Map 3), indicating that this species might be much more widely distributed in Angola than previously considered. One recommendation is that all available historical material assigned to either *A. aculeata* or *A. armata* should be re-examined to document the presence of both species and their respective ranges in Angola. These surveys further provided the first modern record of *Gerrhosaurus auritus* for eastern Angola and have shown that it occurs sympatrically with *Gerrhosaurus nigrolineatus*, noting that the taxonomy of the latter group is still unresolved (Bates et al. 2013). New records were also documented for several rare species (e.g., *Dalophia ellenbergeri*, *Zygaspis nigra*, and *Pelusios bechuanicus*), which are only known from a handful of records within Angola.

Given the robust sampling regime afforded by this study (e.g., 240 trapping nights) additional surveys in southeastern Angola are unlikely to yield many more

species for the Angolan Okavango-Cuando-Zambezi River drainages. At least two additional species (*Typhlacontias gracilis* and *Trachylepis maculilabris*) are expected (Auerbach 1987; Branch 1998; Broadley 1971; Pietersen et al. 2017, 2021). However, ongoing phylogenetic studies on the newly collected material may lead to the description of additional undescribed species, such as in the genus *Panaspis.*

Acknowledgments.—We thank the Wild Bird Trust, which administers the National Geographic Okavango Wilderness Project (2016–2019 National Geographic Society grant). Material was collected and exported under the following export permits issued by the Angolan Ministry of Environment Institute of Biodiversity (MINAMB): 31/GGPCC/2016, 89/INBAC. MINAMB/2017, 002/GGPTBOK/18, 151/INBAC/ MINAMB/2019. Ethical clearance for the study was obtained from the Port Elizabeth (Bayworld) ethics committee (Ethical Clearance nos. 2013 and 2017-2). The project was endorsed and supported by the Governors of Cuando Cubango, Bié, and Moxico provinces. Various colleagues are thanked for collecting herpetological material during their fieldwork, including Alex Rebelo, Roger Bills, Paul Skelton, Maans Booysens, and Kerllen Costa. WC thanks the Eastern Cape Province Department of Sport, Recreation, Arts, and Culture (DSRAC) and Port Elizabeth Museum for granting special leave to take part in these surveys. We thank Enviro-Insight for constructing and donating the drift fences required for the trapping exercise. NLB is currently supported by FCT contract SFRH/PD/BD/140810/2018. We thank the anonymous reviewer for their insightful edits and comments.

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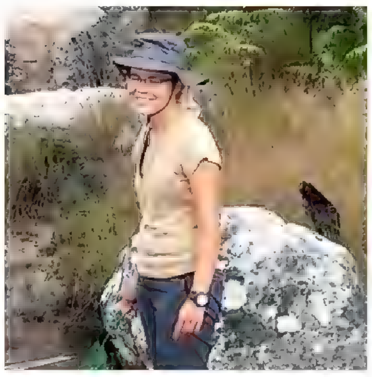

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Amphibian & Reptile Conservation
16(2) [General Section]: 215–236 (e323).

The herpetofauna of Xuan Nha Nature Reserve, Vietnam

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Abstract.*—This article presents the results of a herpetofaunal inventory of Xuan Nha Nature Reserve, Vietnam conducted between April 2016 and May 2021, comprising 41 species of amphibians and 66 species of reptiles, and 82 of the 107 species were recorded directly in this study. One species, *Hemiphyllodactylus bonkowskii*, represents a new record for Son La Province and 20 species of amphibians and reptiles are new records for the Xuan Nha Nature Reserve, comprising 10 species of frogs (*Boulenophrys palpebralespinosa*, *B.* cf. *parva*, *Leptobrachella eos*, *L. ventripunctata*, *Nanohyla marmorata*, *Kurixalus bisacculus*, *Rhacophorus orlovi*, *R. rhodopus*, *Zhangixalus feae*, and *Z. pachyproctus*), two species of lizards (*Hemidactylus garnotii* and *Sphenomorphus indicus*), and eight species of snakes (*Boiga cyanea*, *Dendrelaphis pictus*, *Elaphe taeniura*, *Gonyosoma frenatum*, *Oligodon fasciolatus*, *Hebius chapaensis*, *Rhabdophis nigrocinctus*, and *Pareas hamptoni*). Remarkably, *Gonyosoma coeruleum*, a recently described species from southern China, is recorded for the first time in Vietnam based on a single specimen from Son La Province. The herpetofauna of Xuan Nha Nature Reserve contains a high number of species of conservation concern, including 12 species listed in the Governmental Decree No. 84/2021/ND-CP, 19 species listed in the Vietnam Red Data Book, 18 species listed in the IUCN Red List, and 12 species listed in CITES Appendices. In addition, data on the distribution and natural history of the amphibian and reptile species in Xuan Nha Nature Reserve are provided.

Keywords. Amphibians, biodiversity, distribution, natural history, new records, reptiles

Citation: Pham AV, Nguyen TQ, Pham CT, Sung NB, Le MD, Nguyen TT, Ziegler T. 2022. The herpetofauna of Xuan Nha Nature Reserve, Vietnam. *Amphibian & Reptile Conservation* 16(2) [General Section]: 215–236 (e323).

Accepted: 6 November 2022; **Published:** 31 December 2022

Introduction

Son La Province is located in northwestern Vietnam, bordering Lao PDR in the southwest, and it is covered by 599,000 hectares of natural forest (The People's Committee of Son La Province 2019). Xuan Nha is one of the five nature reserves in Son La Province, located in Moc Chau and Van Ho districts. This nature reserve was established in November 2002 with an area of 18,268 hectares (The People's Committee of Son La Province 2019). The landscape of the nature reserve is characterized by steep and mountainous topography with elevations ranging from 400 to 1,800 m asl.

In terms of the herpetofaunal diversity, Nguyen et al. (2010) provided the first list which included 27 amphibian species and 50 reptile species from Xuan Nha Nature Reserve (NR). Additional new records of reptiles and amphibians from this nature reserve were documented by Nguyen et al. (2017) and Pham et al. (2018, 2020). Most recently, a new species and subspecies of salamander was described from Xuan Nha NR, namely *Tylototriton pasmansi obsti* Bernardes, Le, Nguyen, Pham, Pham, Nguyen, and Ziegler, 2020 (Bernardes et al. 2020). As a result of our ongoing research in the past five years, this article provides an updated list of amphibians and reptiles from Xuan Nha NR, with new data on their distributions and natural history.

Material and Methods

Four field surveys were conducted at eight sites in Xuan Nha NR, Son La Province, Vietnam over a total of 51

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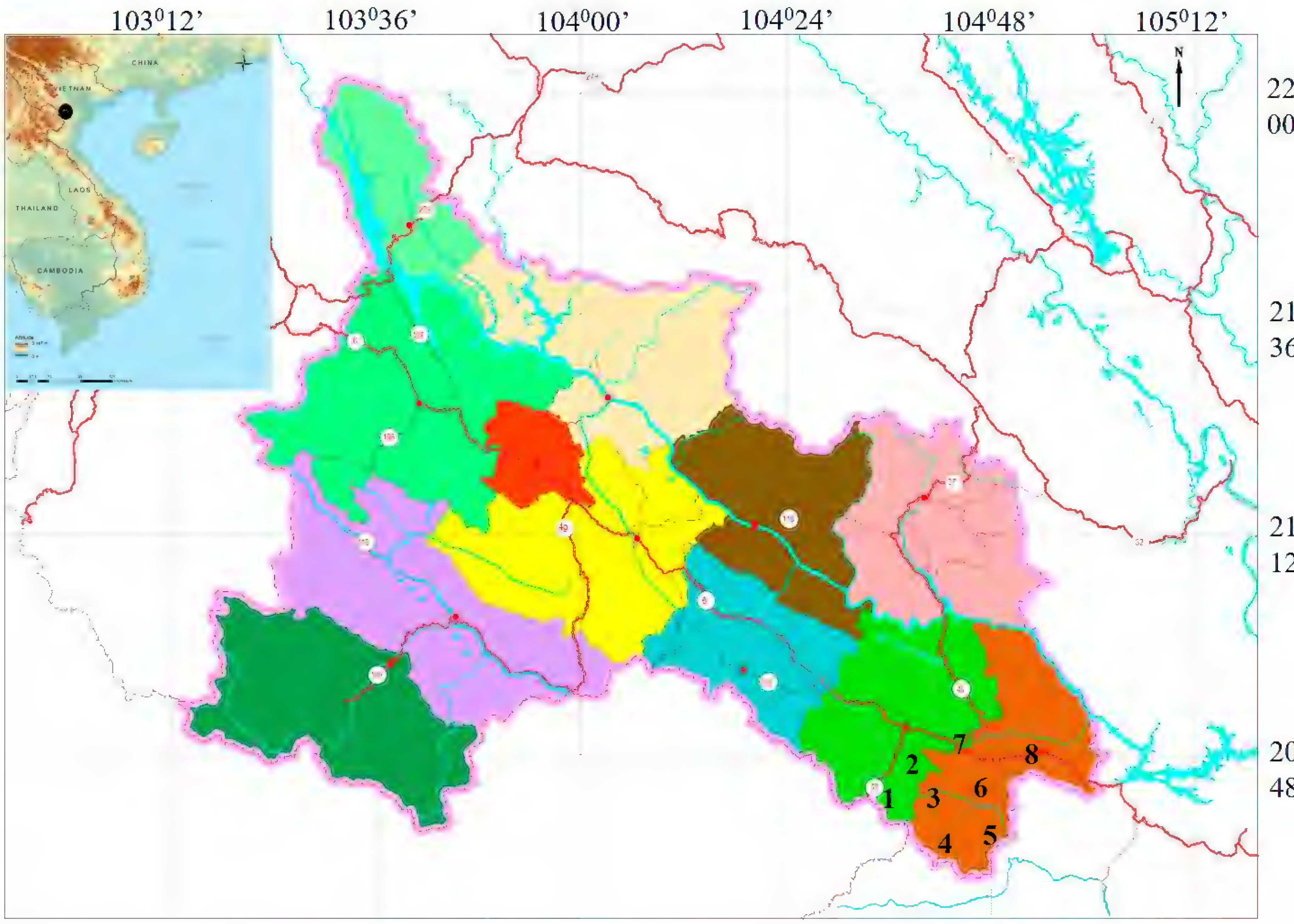

Fig. 1. Survey sites in Xuan Nha Nature Reserve, Son La Province, Viet Nam: 1. Hin Pen Village, Chieng Son Commune; 2. Cong Troi Village, Chieng Son Commune; 3. Kho Hong Village, Chieng Xuan Commune; 4. Lay Village, Tan Xuan Commune; 5. Nga Village, Tan Xuan Commune; 6. Muong An Village, Xuan Nha Commune; 7. Sao Do Village, Van Ho Commune; and 8. So Linh Village, Van Ho Commune.

days. The sites and dates are: **Van Ho District**: from 24 to 27 June 2016 in Kho Hong Village, Chieng Xuan Commune, from 28 June to 2 July 2016 in Muong An Village, Xuan Nha Commune, and from 3 to 6 July 2016 in Sao Do Village, Van Ho Commune, by A.V. Pham and N.B. Sung; from 15 to 20 October 2020 in Kho Hong Village, Chieng Xuan Commune by A.V. Pham, C.V. Hoang, T.Q. Phan, and N.B. Sung; from 20 to 24 April in Sao Do Village, from 25 to 27 April in So Linh Village, Van Ho Commune; from 28 to 30 April 2021 in Muong An Village, Xuan Nha Commune; from 1 April to 3 May 2021 in Lay Village, from 4 to 7 May 2021 in Nga Village, Tan Xuan Commune by A.V. Pham, T. Vaxenh, T.A. Sung, C.A. Sung, and L.A. Sun; **Moc Chau District**: from 15 to 18 June 2017 and from 12 to 14 October 2020 in Hin Pen Village, and from 19 to 24 June 2017 in Cong Troi Village, Chieng Son Commune by A.V. Pham and N.B. Sung (Fig. 1 and Table 1).

The typical habitats at the study sites were undisturbed evergreen forest, disturbed secondary forest, and agricultural areas (Fig. 2). The geographic coordinates (WGS84) were recorded by using a Garmin GPSMAP 62s. Specimens were collected by hand between 0800 and 2300 h. After taking photographs in life, animals were identified to the species level, measured, sexed, and released at the site. For voucher specimens, a few individuals were anaesthetized and euthanized in a closed vessel with a piece of cotton wool containing

Table 1. Information for the survey sites in Xuan Nha Nature Reserve, Vietnam.

No	Site	Latitude	Longitude	Elevation (m)
1	Forest near Hin Pen Village, Chieng Son Commune	20°44.115'N	104°34.113'E	940
2	Forest near Cong Troi Village, Chieng Son Commune	20°45.418'N	104°37.156'E	1,144
3	Forest near Kho Hong Village, Chieng Xuan Commune	20°43.185'N	104°40.267'E	739
4	Forest near Lay Village, Tan Xuan Commune	20°38.015'N	104°40.175'E	850
5	Forest near Nga Village, Tan Xuan Commune	20°37.416'N	104°47.039'E	412
6	Forest near Muong An Village, Xuan Nha Commune	20°44.012'N	104°47.022'E	576
7	Forest near Sao Do Village, Van Ho Commune	20°49.002'N	104°46.132'E	626
8	Forest near So Linh Village, Van Ho Commune	20°46.550'N	104°55.415'E	677

Fig. 2. Habitat types in Xuan Nha Nature Reserve, Vietnam: **(A, A1, A2)** Evergreen forest, **(B)** Agricultural areas, and **(C)** Disturbed secondary forest.

ethyl acetate (Simmon 2002), fixed in 80% ethanol, and then transferred to 70% ethanol for permanent storage. Some road-killed specimens were also collected for morphological examination. These specimens were subsequently deposited in the collection of the Tay Bac University (TBU), Son La Province, Vietnam.

Taxonomic identifications referred to the descriptions in Bain et al. (2003), Boulenger (1893), Bourret (1942), Fei et al. (2012), Hecht et al. (2013), Inger et al. (1999), Smith (1935, 1943), and Taylor (1962). Species names followed Frost (2021) for amphibians and Uetz et al. (2021) for reptiles.

Conservation status levels of amphibian and reptile species followed the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the Red List of International Union for Conservation of Nature and Natural Resources (IUCN), Vietnam Red Data Book (Dang et al. 2007), and The Governmental Decree No. 84/2021/ND-CP, dated on 22 September 2021 by the Government of Vietnam on the management of endangered wild flora and fauna.

Results

A total of 107 species belonging to 75 genera and 26 families were recorded from Xuan Nha NR, comprising 41 species of amphibians (24 genera, seven families) and 66 species of reptiles (51 genera, 19 families) (Table 2). Remarkably, one species of lizard is reported for the first time from Son La Province and 20 additional species are documented for the first time from Xuan Nha NR, comprising 10 species of anurans, two species of lizards, and eight species of snakes. Based on a single snake specimen from Son La Province of Vietnam, we also report the first record of *Gonyosoma coeruleum* outside of its type locality in Yunnan Province, China.

Amphibia
Anura
Bufonidae

Duttaphrynus melanostictus (Schneider, 1799) (Fig. 3A): Individuals were observed at night on the ground in meadowlands, croplands, gardens, and road edges near residential areas.

Megophryidae

Boulenophrys palpebralespinosa (Bourret, 1937) (Fig. 3B): Two specimens were found at night on leaves, 20–50 cm above the ground, near a stream in evergreen forest. This is a new record for Xuan Nha NR.

Boulenophrys cf. *parva* (Boulenger, 1893) (Fig. 3C): One specimen was found at night on the ground, near a stream in evergreen forest. *Boulenophrys parva* seems to be restricted in Myanmar and records of this species in northern Vietnam should be assigned to other named and unnamed species (Manhony et al. 2020).

Leptobrachella eos (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler, and Dubois, 2011) (Fig. 3D): One specimen was found at night on the ground

Table 2. List of amphibian and reptile species recorded from Xuan Nha NR, Vietnam. New record types: ***= new record for Vietnam; ** = new record for Son La Province; * = new record for Xuan Nha NR. **Site**: Descriptions of the sites numbered from 1 to 8 are provided in Table 1. **Habitat** codes: 1 = Evergreen forest, 2 = Disturbed secondary forest, and 3 = Agricultural areas. **Red Data Book** refers to *Red Data Book of Vietnam* (Dang et al. 2007), and **IUCN** refers to *The IUCN Red List of Threatened Species* (IUCN 2021) with the following conservation status codes: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Lower Risk/Near Threatened. **CITES** refers to CITES appendices (2021): I, II = Appendix I and II. **Decree No. 84** refers to *The Governmental Decree No. 84/2021/ND-CP*, dated on 22 September 2021 (The Government of Vietnam 2021), with the following codes: IB = Group IB (Prohibited exploitation and use for commercial purpose); IIB = Group IIB (limited exploitation and use for commercial purpose). **Record evidence**: The types of observations made for each species in the field surveys of this study. **Previous record** codes indicate literature references: 1 = Nguyen et al. (2010), 2 = Nguyen et al. (2017), 3 = Pham et al. (2018), 4 = Bernardes et al. (2020), 5 = Pham et al. (2020), and 6 = Pham et al. (2022).

No.	Name	Site	Habitat	Red Data Book	IUCN	CITES	Decree No. 84	Record evidence (this study)	Previous record
ANURA									
Bufonidae Gray, 1825									
1	*Duttaphrynus melanostictus* (Schneider, 1799)	1–8	2, 3					Photos	1
Megophryidae Bonaparte, 1850									
2	*Boulenophrys palpebralespinosa* (Bourret, 1937)*	4	1	CR				Specimens (2)	
3	*Boulenophrys* cf. *parva* (Boulenger, 1893)*	4	1					Specimen (1)	
4	*Leptobrachella eos* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler, and Dubois, 2011)*	4	1					Specimen (1)	
5	*Leptobrachella namdongensis* Hoang, Nguyen, Luu, Nguyen, and Jiang, 2019	4	1		EN			Specimens (4)	6
6	*Leptobrachella ventripunctata* (Fei, Ye, and Li, 1990)*	3	1					Specimens (3)	
7	*Leptobrachium masatakasatoi* Matsui, 2013	5	1					Specimens (2)	1
8	*Xenophrys maosonensis* (Bourret, 1937)	5	1					Specimens (2)	1
Microhylidae Günther, 1858 (1843)									
9	*Kaloula pulchra* Gray, 1831	1	3					Photos	1
10	*Microhyla berdmorei* (Blyth, 1856)								1
11	*Microhyla butleri* Boulenger, 1900	2, 3, 6	3					Specimen (1) Photos	1
12	*Microhyla heymonsi* Vogt, 1911	3, 4, 5, 7, 8	2, 3					Specimens (2) Photos	1
13	*Microhyla mukhlesuri* Hasan, Islam, Kuramoto, Kurabayashi, and Sumida, 2014	2, 5–8	3					Specimen (1) Photos	1
14	*Microhyla pulchra* (Hallowell, 1861)	1, 4, 5, 7, 8	3					Specimens (2) Photos	1
15	*Nanohyla marmorata* (Bain and Nguyen, 2004)*	3	1					Specimens (2)	
Dicroglossidae Anderson, 1871									
16	*Fejervarya limnocharis* (Gravenhost, 1829)	1–8	2, 3					Photos	1

Table 2 (continued). List of amphibian and reptile species recorded from Xuan Nha NR, Vietnam. New record types: ***= new record for Vietnam; ** = new record for Son La Province; * = new record for Xuan Nha NR. **Site**: Descriptions of the sites numbered from 1 to 8 are provided in Table 1. **Habitat** codes: 1 = Evergreen forest, 2 = Disturbed secondary forest, and 3 = Agricultural areas. **Red Data Book** refers to *Red Data Book of Vietnam* (Dang et al. 2007), and **IUCN** refers to *The IUCN Red List of Threatened Species* (IUCN 2021) with the following conservation status codes: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Lower Risk/Near Threatened. **CITES** refers to CITES appendices (2021): I, II = Appendix I and II. **Decree No. 84** refers to *The Governmental Decree No. 84/2021/ND-CP*, dated on 22 September 2021 (The Government of Vietnam 2021), with the following codes: IB = Group IB (Prohibited exploitation and use for commercial purpose); IIB = Group IIB (limited exploitation and use for commercial purpose). **Record evidence**: The types of observations made for each species in the field surveys of this study. **Previous record** codes indicate literature references: 1 = Nguyen et al. (2010), 2 = Nguyen et al. (2017), 3 = Pham et al. (2018), 4 = Bernardes et al. (2020), 5 = Pham et al. (2020), and 6 = Pham et al. (2022).

No.	Name	Site	Habitat	Red Data Book	IUCN	CITES	Decree No. 84	Record evidence (this study)	Previous record
17	*Hoplobatrachus rugulosus* (Wiegmann, 1834)	1, 3, 5–7	3					Photos	1
18	*Limnonectes bannaensis* Ye, Fei, Xie, and Jiang, 2007	1, 3, 4, 6, 8	1, 2					Photos	1
19	*Occidozyga lima* (Gravenhorst, 1829)								1
20	*Occidozyga martensii* (Peters, 1867)								1
21	*Quasipaa verrucospinosa* (Bourret, 1937)	1, 3, 4	1					Photos	1
Ranidae Batsch, 1796									
22	*Amolops cremnobatus* Inger and Kottelat, 1998	4	1					Specimens (2)	6
23	*Hylarana macrodactyla* Gunther, 1858								1
24	*Hylarana taipehensis* (Van Denburgh, 1909)								1
25	*Nidirana chapaensis* (Bourret, 1937)	3	1					Specimen (1) Photos	6
26	*Odorrana chloronota* (Günther, 1876)								1
27	*Odorrana nasica* (Boulenger, 1903)	5	1					Specimen (1)	1
28	*Odorrana tiannanensis* (Yang and Li, 1980)	3	1					Specimens (2)	6
29	*Rana johnsi* Smith, 1921	1	2					Specimen (1)	1
30	*Sylvirana guentheri* (Boulenger, 1882)	1, 3, 4, 6, 7	3					Photos	1
31	*Sylvirana maosonensis* (Bourret, 1937)	5	1					Specimen (1)	1
32	*Sylvirana nigrovittata* (Blyth, 1856)	1, 3, 5	1, 2					Specimen (1) Photos	1
Rhacophoridae Hoffman, 1932 (1858)									
33	*Kurixalus bisacculus* (Taylor, 1962)*	1–5	1, 2					Specimen (1) Photos	
34	*Polypedates megacephalus* Hallowell, 1861	1–8	1–3					Specimens (2) Photos	1
35	*Raorchestes parvulus* (Boulenger, 1893)	3, 4, 6	1					Specimens (2) Photos	6
36	*Rhacophorus kio* Ohler and Delorme, 2006	3, 4	1	EN				Photos	1
37	*Rhacophorus orlovi* Ziegler and Köhler, 2001*	3, 4, 8	1					Specimens (3) Photos	

Table 2 (continued). List of amphibian and reptile species recorded from Xuan Nha NR, Vietnam. New record types: ***= new record for Vietnam; ** = new record for Son La Province; * = new record for Xuan Nha NR. **Site**: Descriptions of the sites numbered from 1 to 8 are provided in Table 1. **Habitat** codes: 1 = Evergreen forest, 2 = Disturbed secondary forest, and 3 = Agricultural areas. **Red Data Book** refers to *Red Data Book of Vietnam* (Dang et al. 2007), and **IUCN** refers to *The IUCN Red List of Threatened Species* (IUCN 2021) with the following conservation status codes: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Lower Risk/Near Threatened. **CITES** refers to CITES appendices (2021): I, II = Appendix I and II. **Decree No. 84** refers to *The Governmental Decree No. 84/2021/ND-CP*, dated on 22 September 2021 (The Government of Vietnam 2021), with the following codes: IB = Group IB (Prohibited exploitation and use for commercial purpose); IIB = Group IIB (limited exploitation and use for commercial purpose). **Record evidence**: The types of observations made for each species in the field surveys of this study. **Previous record** codes indicate literature references: 1 = Nguyen et al. (2010), 2 = Nguyen et al. (2017), 3 = Pham et al. (2018), 4 = Bernardes et al. (2020), 5 = Pham et al. (2020), and 6 = Pham et al. (2022).

No.	Name	Site	Habitat	Red Data Book	IUCN	CITES	Decree No. 84	Record evidence (this study)	Previous record
38	*Rhacophorus rhodopus* Liu and Hu, 1960*	3, 4	1					Photos	
39	*Zhangixalus feae* (Boulenger, 1893)*	3	1	EN				Photos	
40	*Zhangixalus pachyproctus* Yu, Hui, Hou, Wu, Rao, and Yang, 2019*	3, 5	1					Photos	
CAUDATA									
Salamandridae Goldfuss, 1820									
41	*Tylototriton pasmansi obsti* Bernardes, Le, Nguyen, Pham, Pham, Nguyen, and Ziegler, 2020	3, 8	1			II	IIB	Photos	4
SQUAMATA									
Agamidae									
42	*Acanthosaura lepidogaster* (Cuvier, 1829)	1, 2, 8	1					Photos	1
43	*Calotes emma* Gray, 1845	8	1					Specimen (1)	1
44	*Calotes versicolor* (Daudin, 1802)	1–8	3					Specimen (1) Photos	1
45	*Draco maculatus* (Gray, 1845)								1
46	*Physignathus cocincinus* Cuvier, 1829			VU	VU				1
Gekkonidae									
47	*Cyrtodactylus otai* Nguyen, Le, Pham, Ngo, Hoang, Pham, and Ziegler, 2015	7, 8	2		EN			Photos	2
48	*Gekko palmatus* Boulenger, 1907	3, 8	2					Specimen (1) Photos	3
49	*Gekko reevesii* (Gray, 1831)	7, 8	2					Photos	1
50	*Hemidactylus frenatus* Duméril and Bibron, 1836	1–8	3					Photos	1
51	*Hemidactylus garnotii* Duméril and Bibron, 1836*	6	2					Specimen (1) Photos	
52	*Hemiphyllodactylus bonkowskii* Nguyen, Do, Ngo, Pham, Pham, Le, and Ziegler, 2020**	8	2					Specimens (2)	

Table 2 (continued). List of amphibian and reptile species recorded from Xuan Nha NR, Vietnam. New record types: ***= new record for Vietnam; ** = new record for Son La Province; * = new record for Xuan Nha NR. **Site**: Descriptions of the sites numbered from 1 to 8 are provided in Table 1. **Habitat** codes: 1 = Evergreen forest, 2 = Disturbed secondary forest, and 3 = Agricultural areas. **Red Data Book** refers to *Red Data Book of Vietnam* (Dang et al. 2007), and **IUCN** refers to *The IUCN Red List of Threatened Species* (IUCN 2021) with the following conservation status codes: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Lower Risk/Near Threatened. **CITES** refers to CITES appendices (2021): I, II = Appendix I and II. **Decree No. 84** refers to *The Governmental Decree No. 84/2021/ND-CP*, dated on 22 September 2021 (The Government of Vietnam 2021), with the following codes: IB = Group IB (Prohibited exploitation and use for commercial purpose); IIB = Group IIB (limited exploitation and use for commercial purpose). **Record evidence**: The types of observations made for each species in the field surveys of this study. **Previous record** codes indicate literature references: 1 = Nguyen et al. (2010), 2 = Nguyen et al. (2017), 3 = Pham et al. (2018), 4 = Bernardes et al. (2020), 5 = Pham et al. (2020), and 6 = Pham et al. (2022).

No.	Name	Site	Habitat	Red Data Book	IUCN	CITES	Decree No. 84	Record evidence (this study)	Previous record
Lacertidae									
53	*Takydromus sexlineatus* Daudin, 1802	2	2					Specimen (1)	1
Scincidae									
54	*Eutropis chapaensis* (Bourret, 1937)								1
55	*Eutropis longicaudatus* (Hallowell, 1857)	1, 2, 6	3					Photos	1
56	*Eutropis multifasciatus* (Kuhl, 1820)	4, 5, 7	3					Photos	1
57	*Sphenomorphus indicus* (Gray, 1853)*	8	1					Specimen (1)	
58	*Tropidophorus baviensis* Bourret, 1939	7	2					Specimen (1)	1
Varanidae									
59	*Varanus salvator* (Laurenti, 1768)			EN		II	IIB		1
Typhlopidae									
60	*Indotyphlops braminus* (Daudin, 1803)	6	2					Specimen (1)	1
Pythonidae									
61	*Python molurus* (Linnaeus, 1758)			CR	NT	II	IIB		1
Xenopeltidae									
62	*Xenopeltis unicolor* Reinwardt, 1827	1, 6	3					Specimen (1) Photos	1
Colubridae									
63	*Ahaetulla prasina* (Boie, 1827)	2	2					Photos	1
64	*Boiga cyanea* (Duméril, Bibron, and Duméril, 1854)*	7	1					Specimen (1)	
65	*Boiga guangxiensis* Wen, 1998	4	1					Photos	5
66	*Boiga multomaculata* (Boie, 1827)	3	2					Photos	1
67	*Calamaria pavimentata* Duméril, Bibron, and Duméril, 1854	1	2					Specimen (1)	1
68	*Coelognathus radiatus* (Boie, 1827)	7	3	EN				Photos	1

Table 2 (continued). List of amphibian and reptile species recorded from Xuan Nha NR, Vietnam. New record types: ***= new record for Vietnam; ** = new record for Son La Province; * = new record for Xuan Nha NR. **Site**: Descriptions of the sites numbered from 1 to 8 are provided in Table 1. **Habitat** codes: 1 = Evergreen forest, 2 = Disturbed secondary forest, and 3 = Agricultural areas. **Red Data Book** refers to *Red Data Book of Vietnam* (Dang et al. 2007), and **IUCN** refers to *The IUCN Red List of Threatened Species* (IUCN 2021) with the following conservation status codes: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Lower Risk/Near Threatened. **CITES** refers to CITES appendices (2021): I, II = Appendix I and II. **Decree No. 84** refers to *The Governmental Decree No. 84/2021/ND-CP*, dated on 22 September 2021 (The Government of Vietnam 2021), with the following codes: IB = Group IB (Prohibited exploitation and use for commercial purpose); IIB = Group IIB (limited exploitation and use for commercial purpose). **Record evidence**: The types of observations made for each species in the field surveys of this study. **Previous record** codes indicate literature references: 1 = Nguyen et al. (2010), 2 = Nguyen et al. (2017), 3 = Pham et al. (2018), 4 = Bernardes et al. (2020), 5 = Pham et al. (2020), and 6 = Pham et al. (2022).

No.	Name	Site	Habitat	Red Data Book	IUCN	CITES	Decree No. 84	Record evidence (this study)	Previous record
69	*Dendrelaphis pictus* (Gmelin, 1789)*	1, 8	2					Specimens (2) Photos	
70	*Elaphe moellendorffi* (Boettger, 1886)	8	2	VU	VU			Photos	1
71	*Elaphe taeniura* (Cope, 1861)*	1, 2	2, 3		VU			Photos	
72	*Euprepiophis mandarinus* (Cantor, 1842)	3	1	VU				Specimen (1)	1
73	*Gonyosoma coeruleum* Liu, Hou, Lwin, Wang, and Rao, 2021***	5	2					Specimen (1)	
74	*Gonyosoma frenatum* (Gray, 1853)*	8	1					Specimen (1)	
75	*Lycodon futsingensis* (Pope, 1928)	5	1					Specimen (1)	1
76	*Lycodon meridionalis* (Bourret, 1935)	7	2					Specimen (1)	5
77	*Oligodon fasciolatus* (Günther, 1864)*	2, 6	2					Specimen (1) Photos	
78	*Oreocryptophis porphyraceus* (Cantor, 1839)	7	2	VU				Photos	1
79	*Ptyas korros* (Schlegel, 1837)	1, 5, 6	2, 3	EN	NT			Photos	1
80	*Ptyas mucosa* (Linnaeus, 1758)			EN		II	IIB		1
Elapidae									
81	*Bungarus fasciatus* (Schneider, 1801)	5	2	EN				Photos	1
82	*Bungarus wanghaotingi* Pope, 1928	1, 6	2					Photos	1
83	*Naja atra* Cantor, 1842	7	2	EN	VU	II	IIB	Photos	1
84	*Ophiophagus hannah* (Cantor, 1836)			CR	VU	II	IB		1
85	*Sinomicrurus macclellandi* (Reinhardt, 1844)	3	1					Specimen (1)	1
Homalopsidae									
86	*Hypsiscopus plumbea* (Boie, 1827)								1
Pseudaspididae									
87	*Psammodynastes pulverulentus* (Boie, 1827)	7	2					Photos	1

Table 2 (continued). List of amphibian and reptile species recorded from Xuan Nha NR, Vietnam. New record types: ***= new record for Vietnam; ** = new record for Son La Province; * = new record for Xuan Nha NR. **Site**: Descriptions of the sites numbered from 1 to 8 are provided in Table 1. **Habitat** codes: 1 = Evergreen forest, 2 = Disturbed secondary forest, and 3 = Agricultural areas. **Red Data Book** refers to *Red Data Book of Vietnam* (Dang et al. 2007), and **IUCN** refers to *The IUCN Red List of Threatened Species* (IUCN 2021) with the following conservation status codes: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Lower Risk/Near Threatened. **CITES** refers to CITES appendices (2021): I, II = Appendix I and II. **Decree No. 84** refers to *The Governmental Decree No. 84/2021/ND-CP*, dated on 22 September 2021 (The Government of Vietnam 2021), with the following codes: IB = Group IB (Prohibited exploitation and use for commercial purpose); IIB = Group IIB (limited exploitation and use for commercial purpose). **Record evidence**: The types of observations made for each species in the field surveys of this study. **Previous record** codes indicate literature references: 1 = Nguyen et al. (2010), 2 = Nguyen et al. (2017), 3 = Pham et al. (2018), 4 = Bernardes et al. (2020), 5 = Pham et al. (2020), and 6 = Pham et al. (2022).

No.	Name	Site	Habitat	Red Data Book	IUCN	CITES	Decree No. 84	Record evidence (this study)	Previous record
Natricidae									
88	*Amphiesma stolatum* (Linnaeus, 1758)								1
89	*Fowlea flavipunctatus* (Hallwell, 1861)								1
90	*Hebius chapaensis* (Bourret, 1934)*	4	1					Specimen (1)	
91	*Rhabdophis chrysargos* (Schlegel, 1837)								1
92	*Rhabdophis nigrocinctus* (Blyth, 1856)*	6	1					Specimen (1)	
93	*Rhabdophis helleri* (Schmidt, 1925)	1, 2, 6, 7	2, 3					Photos	1
94	*Trimerodytes percarinatus* (Boulenger, 1899)	3	1					Photos	1
Pareidae									
95	*Pareas hamptoni* (Boulenger, 1905)*	7	1					Specimen (1)	
Viperidae									
96	*Ovophis monticola* (Günther, 1864)	4	1					Specimen (1)	1
97	*Trimeresurus albolabris* Gray, 1842	4, 6, 7	2					Specimen (1) Photos	1
98	*Trimeresurus stejnegeri* Schmidt, 1925								1
TESTUDINES									
Platystermidae									
99	*Platysternon megacephalum* Gray, 1831	4	1	EN	CR	I	IB	Photos	1
Geoemydidae									
100	*Cuora galbinifrons* Bourret, 1939			EN	CR	II	IB		1
101	*Cuora mouhotii* (Gray, 1862)				EN	II	IIB		1
102	*Geoemyda spengleri* (Gmelin, 1789)				EN	II	IIB		1
103	*Mauremys sinensis* (Gray, 1834)				CR				1
104	*Sacalia quadriocellata* (Siebenrock, 1903)				CR	II	IIB		1

Table 2 (continued). List of amphibian and reptile species recorded from Xuan Nha NR, Vietnam. New record types: ***= new record for Vietnam; ** = new record for Son La Province; * = new record for Xuan Nha NR. **Site**: Descriptions of the sites numbered from 1 to 8 are provided in Table 1. **Habitat** codes: 1 = Evergreen forest, 2 = Disturbed secondary forest, and 3 = Agricultural areas. **Red Data Book** refers to *Red Data Book of Vietnam* (Dang et al. 2007), and **IUCN** refers to *The IUCN Red List of Threatened Species* (IUCN 2021) with the following conservation status codes: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Lower Risk/Near Threatened. **CITES** refers to CITES appendices (2021): I, II = Appendix I and II. **Decree No. 84** refers to *The Governmental Decree No. 84/2021/ND-CP*, dated on 22 September 2021 (The Government of Vietnam 2021), with the following codes: IB = Group IB (Prohibited exploitation and use for commercial purpose); IIB = Group IIB (limited exploitation and use for commercial purpose). **Record evidence**: The types of observations made for each species in the field surveys of this study. **Previous record** codes indicate literature references: 1 = Nguyen et al. (2010), 2 = Nguyen et al. (2017), 3 = Pham et al. (2018), 4 = Bernardes et al. (2020), 5 = Pham et al. (2020), and 6 = Pham et al. (2022).

No.	Name	Site	Habitat	Red Data Book	IUCN	CITES	Decree No. 84	Record evidence (this study)	Previous record
Testudinidae									
105	*Indotestudo elongata* (Blyth, 1853)			EN	CR	II	IIB		1
106	*Manouria impressa* (Guenther, 1882)	3	1	VU	EN	II	IIB	Photos	1
Trionychidae									
107	*Palea steindachneri* (Siebenrock, 1906)			VU	CR	II	IIB		1

near a stream in evergreen forest. This is a new record for Xuan Nha NR.

Leptobrachella namdongensis Hoang, Nguyen, Luu, Nguyen, and Jiang, 2019 (Fig. 3E): Four specimens were found at night on the ground or on stones near a stream. The surrounding habitat was evergreen forest, composed of small hardwoods, liane, and shrub.

Leptobrachella ventripunctata (Fei, Ye, and Li, 1990) (Fig. 3F): One specimen was found on a stone near a stream and two other specimens were observed along a forest path at night. This is a new record for Xuan Nha NR.

Leptobrachium masatakasatoi Matsui, 2013 (Fig. 3G): Two specimens were found at night on the ground near a stream in evergreen forest.

Xenophrys maosonensis (Bourret, 1937) (Fig. 3H): Two specimens were found at night on the ground, near a stream in evergreen forest.

Microhylidae

Kaloula pulchra Gray, 1831 (Fig. 3I): An individual was observed at night on a bonsai pot in a household garden.

Microhyla butleri Boulenger, 1900 (Fig. 3J): One specimen was found at night on the ground in meadowlands and other individuals were observed at night in croplands, and at small puddle edges near the rice fields and forest edges.

Microhyla heymonsi Vogt, 1911 (Fig. 3K): Two specimens were found at night on the ground along road edges and other individuals were observed at night on the ground in croplands, in meadowlands, croplands, and forest trails near forest edges, and inside the forest.

Microhyla mukhlesuri Hasan, Islam, Kuramoto, Kurabayashi, and Sumida, 2014 (Fig. 3L): One specimen was found at night on the ground near small puddle edges in rice fields, and other individuals were observed at night on the ground near small puddle edges in rice fields, meadowlands, and croplands.

Microhyla pulchra (Hallowell, 1861) (Fig. 3M): Two specimens were found at night on the ground in meadowlands near rice fields, and other individuals were observed at night on the ground in croplands, around small puddle edges.

Nanohyla marmorata (Bain and Nguyen, 2004) (Fig. 3N): Two specimens were found in the morning on the forest path. The surrounding habitat was evergreen forest. This is a new record for Xuan Nha NR.

Dicroglossidae

Fejervarya limnocharis (Gravenhost, 1829) (Fig. 3O): Many individuals were observed at night on the ground, in meadowlands near rice fields, croplands, and small puddles at road edges.

Hoplobatrachus rugulosus (Wiegmann, 1834) (Fig. 3P): Individuals were observed at night on the ground, at pond edges, and in rice fields.

Limnonectes bannaensis Ye, Fei, Xie, and Jiang, 2007 (Fig. 3Q): Individuals were observed at night on the ground near streams or water edges in streams in evergreen forest.

Quasipaa verrucospinosa (Bourret, 1937) (Fig. 3R): Individuals were observed at night on rocks in streams or near waterfalls. The surrounding habitat was evergreen forest.

Ranidae

Amolops cremnobatus Inger and Kottelat, 1998 (Fig.

Fig. 3. Amphibian species recorded in Xuan Nha Nature Reserve, Vietnam: **(A)** *Duttaphrynus melanostictus,* **(B)** *Boulenophrys palpebralespinosa,* **(C)** *Boulenophrys* cf. *parva,* **(D)** *Leptobrachella eos,* **(E)** *L. namdongensis,* **(F)** *L. ventripunctata,* **(G)** *Leptobrachium masatakasatoi,* **(H)** *Xenophrys maosonensis,* **(I)** *Kaloula pulchra*, **(J)** *Microhyla butleri*, **(K)** *M. heymonsi*, **(L)** *M. mukhlesuri,* **(M)** *M. pulchra,* **(N)** *Nanohyla marmorata,* **(O)** *Fejervarya limnocharis,* **(P)** *Hoplobatrachus rugulosus,* **(Q)** *Limnonectes bannaensis,* and **(R)** *Quasipaa verrucospinosa.*

Fig. 4. Additional amphibian species recorded in Xuan Nha Nature Reserve, Vietnam: **(A)** *Amolops cremnobatus,* **(B)** *Nidirana chapaensis,* **(C)** *Odorrana nasica,* **(D)** *O. tiannanensis,* **(E)** *Rana johnsi,* **(F)** *Sylvirana guentheri,* **(G)** *S. maosonensis,* **(H)** *S. nigrovittata,* **(I)** *Kurixalus bisacculus,* **(J)** *Polypedates megacephalus,* **(K)** *Raorchestes parvulus,* **(L)** *Rhacophorus kio,* **(M)** *R. orlovi,* **(N)** *Rhacophorus rhodopus,* **(O)** *Zhangixalus feae,* **(P)** *Z. pachyproctus,* and **(Q)** *Tylototriton pasmansi obsti.*

4A): Two specimens were found at night on rocks in streams with strong currents. The surrounding habitat was evergreen forest, composed of small hardwoods, liane, and shrub.

Nidirana chapaensis (Bourret, 1937) (Fig. 4B): One specimen was found at night on tree leaves, 30 cm above the ground, near a stream. Two other individuals were observed on the ground at a small puddle edge in evergreen forest.

Odorrana nasica (Boulenger, 1903) (Fig. 4C): One specimen was found at night on a rock near a waterfall in evergreen forest.

Odorrana tiannanensis (Yang and Li, 1980) (Fig. 4D): Two specimens were found at night on the ground near a stream in evergreen forest.

Rana johnsi Smith, 1921 (Fig. 4E): One specimen was found at night on the ground near a stream at the forest edge.

Sylvirana guentheri (Boulenger, 1882) (Fig. 4F): Individuals were observed at night on the ground or on leaves, ca. 30–50 cm above the ground near pond edges and streams. The surrounding habitat was rice field.

Sylvirana maosonensis (Bourret, 1937) (Fig. 4G): One specimen was found at night on the ground near a stream in evergreen forest.

Sylvirana nigrovittata (Blyth, 1856) (Fig. 4H): One specimen was found at night on the ground near a stream, and other individuals were observed at night on the ground, on stones near a stream or at the water edges in streams. The surrounding habitat was evergreen forest. The call concerts were regularly heard in the evening.

Rhacophoridae

Kurixalus bisacculus (Taylor, 1962) (Fig. 4I): One specimen was found at night on a tree branch near a stream, and other individuals were observed at night while sitting on leaves near a stream or near puddles, ca. 1–2 m above the ground. The surrounding habitat was mixed evergreen forest of small hardwoods, bamboo, and shrubs. This is a new record for Xuan Nha NR.

Polypedates megacephalus Hallowell, 1861 (Fig. 4J): Two specimens were found at night on the tree branches near puddles, and other individuals were observed at night while sitting on leaves or branches near streams, puddles, and ponds, ca. 0.3–2 m above the ground. The surrounding habitat was cultivated land, mixed evergreen forest of small hardwoods, bamboo, and shrubs.

Raorchestes parvulus (Boulenger, 1893) (Fig. 4K): Two specimens were found at night sitting on leaves near streams, ca. 1–3 m above the ground in evergreen forest.

Rhacophorus kio Ohler and Delorme, 2006 (Fig. 4L): Individuals were observed at night while sitting on leaves near puddles, ca. 2–5 m above the ground in evergreen forest.

Rhacophorus orlovi Ziegler and Köhler, 2001 (Fig. 4M): Three specimens were found at night while sitting on leaves near streams, 2–3 m above the ground in evergreen forest. This is a new record for Xuan Nha NR.

Rhacophorus rhodopus Liu and Hu, 1960 (Fig. 4N): Individuals were observed at night while sitting on leaves near puddles, ca. 2–5 m above the ground in evergreen forest. This is a new record for Xuan Nha NR.

Zhangixalus feae (Boulenger, 1893) (Fig. 4O): Individuals were observed at night while sitting on leaves, 0.5–3 m above the ground; some individuals found on the ground near streams in evergreen forest.

Zhangixalus pachyproctus Yu, Hui, Hou, Wu, Rao, and Yang, 2019 (Fig. 4P): Individuals were observed at night while sitting on leaves, ca. 1–6 m above the ground, near large puddles in evergreen forest. This is a new record for Xuan Nha NR.

Caudata
Salamandridae

Tylototriton pasmansi obsti Bernardes, Le, Nguyen, Pham, Pham, Nguyen, and Ziegler, 2020 (Fig. 4Q): Individuals were observed during the daytime in small streams in evergreen forest. Surrounding habitat was small hardwoods, bamboo, and shrub.

Reptilia
Squamata
Agamidae

Acanthosaura lepidogaster (Cuvier, 1829) (Fig. 5A): An individual was observed while sitting on a tree, about 2 m above the ground, and another individual was seen while crossing a forest path.

Calotes emma Gray, 1845 (Fig. 5B): One specimen was found in the morning on a forest path in evergreen forest.

Calotes versicolor (Daudin, 1802) (Fig. 5C): Individuals were observed during the daytime near cultivated areas and another road-killed individual was found on Road 102. Some individuals were seen on the ground near bushes in a garden.

Gekkonidae

Cyrtodactylus otai Nguyen, Le, Pham, Ngo, Hoang, Pham, and Ziegler, 2015 (Fig. 5D): Three individuals were observed at night, on tree branches, near limestone cliffs at the forest edges.

Gekko palmatus Boulenger, 1907 (Fig. 5E): One specimen was found and other individuals were observed at night on limestone cliffs at the forest edges.

Fig. 5. Lizard species recorded in Xuan Nha Nature Reserve, Vietnam: **(A)** *Acanthosaura lepidogaster*, **(B)** *Calotes emma,* **(C)** *C. versicolor,* **(D)** *Cyrtodactylus otai,* **(E)** *Gekko palmatus,* **(F)** *G. reevesii,* **(G)** *Hemidactylus frenatus,* **(H)** *H. garnotii,* **(I)** *Hemiphyllodactylus bonkowskii,* **(J)** *Takydromus sexlineatus,* **(K)** *Eutropis longicaudatus,* **(L)** *E. multifasciatus,* **(M)** *Sphenomorphus indicus,* and **(N)** *Tropidophorus baviensis.*

Gekko reevesii (Gray, 1831) (Fig. 5F): An individual was observed at night on limestone cliffs, and another individual was observed on a big tree, about 5 m above the ground.

Hemidactylus frenatus Duméril and Bibron, 1836 (Fig. 5G): Individuals were observed at night on the wall near a light in a residential area.

Hemidactylus garnotii Duméril and Bibron, 1836 (Fig. 5H): One specimen was found and other individuals were observed at night on limestone karst outcrops, 2–3 m above the ground. The surrounding habitat was secondary forest. This is a new record for Xuan Nha NR.

Hemiphyllodactylus bonkowskii Nguyen, Do, Ngo, Pham, Pham, Le, and Ziegler, 2020 (Fig. 5I): Two specimens were found at night on tree branches near limestone cliffs at forest edges. This is a new record for Xuan Nha NR and Son La Province.

Lacertidae

Takydromus sexlineatus Daudin, 1802 (Fig. 5J): One specimen was found during the daytime, on the ground near bamboo trees in secondary forest.

Scincidae

Eutropis longicaudatus (Hallowell, 1857) (Fig. 5K): Individuals were found during the daytime on the ground, garden fences, road edges, and shrubs near cultivated areas.

Eutropis multifasciatus (Kuhl, 1820) (Fig. 5L): Three individuals were found during the daytime on the ground, along road edges near cultivated areas.

Sphenomorphus indicus (Gray, 1853) (Fig. 5M): One specimen was found in the afternoon on a forest path in evergreen forest. This is a new record for Xuan Nha NR.

Tropidophorus baviensis Bourret, 1939 (Fig. 5N): One specimen was found under a carpet of fallen leaves at the forest edge.

Typhlopidae

Indotyphlops braminus (Daudin, 1803) (Fig. 6A): One specimen was found in the morning under a rotten bamboo tree at the forest edge.

Xenopeltidae

Xenopeltis unicolor Reinwardt, 1827 (Fig. 6B): An individual was observed in the afternoon under a rotten plank in a garden and another road-killed specimen was found on Road 102.

Colubridae

Ahaetulla prasina (Boie, 1827) (Fig. 6C): An individual was found at night on the thick grass in secondary forest.

Boiga cyanea (Duméril, Bibron, and Duméril, 1854) (Fig. 6D): A road-killed specimen was found in the afternoon on Road 102. The surrounding habitat was evergreen forest.

Boiga guangxiensis Wen, 1998 (Fig. 6E): An individual was observed at night on a tree branch near a stream in evergreen forest.

Boiga multomaculata (Boie, 1827) (Fig. 6F): An individual was observed at night while moving on the grass near a stream at the forest edge.

Calamaria pavimentata Duméril, Bibron, and Duméril, 1854 (Fig. 6G): A road-killed individual was found in the morning on Road 102. The surrounding habitat was secondary forest.

Coelognathus radiatus (Boie, 1827) (Fig. 6H): An individual was observed in the afternoon while moving across Road 102.

Dendrelaphis pictus (Gmelin, 1789) (Fig. 6I): Two specimens were found in the afternoon near Road 102, an individual crawling on a tree branch and a road-killed individual on Highway 6. This is a new record for Xuan Nha NR.

Elaphe moellendorffi (Boettger, 1886) (Fig. 6J): An individual was observed in the afternoon near the entrance of a cave at the forest edge.

Elaphe taeniura (Cope, 1861) (Fig. 6K): An individual was observed in the morning near a large rock at the forest edge, and another individual was detected in an agricultural area. This is a new record for Xuan Nha NR.

Euprepiophis mandarinus (Cantor, 1842) (Fig. 6L): A road-killed individual was found in the morning on Highway 6. The surrounding habitat was evergreen forest.

Gonyosoma coeruleum Liu, Hou, Lwin, Wang, and Rao 2021 (Fig. 6M): A road-killed specimen (adult male) was found in the morning on Highway 6. The surrounding habitat was evergreen forest. This is the first record of this species in Vietnam. *Gonyosoma coeruleum* was recently described by Liu et al. (2021) from Yunnan Province, China. The new species closely resembles *G. prasinum* (Blyth), but it is differentiated from the latter species by having the precloacal plate divided, iris blue and inside of mouth greyish-white in life. Morphological characteristics of the specimen from Son La Province are as follows: Snout-vent length: 662 mm; tail length: 242 mm; head distinguished from neck; pupil rounded; rostral broader than high; internasals as wide as long; prefrontal shorter than length of frontal; frontal pentagonal; parietals longer than wide; nasal paired; loreal 1/1; supralabials 9/9, fourth to sixth entering orbit; infralabials 10/10, first to fifth bordering chin shields; preocular 1/1; postoculars 2/2; anterior temporals 2/2, posterior temporals 2/2; dorsal scale

Fig. 6. Snake species recorded in Xuan Nha Nature Reserve, Vietnam: **(A)** *Indotyphlops braminus,* **(B)** *Xenopeltis unicolor,* **(C)** *Ahaetulla prasina,* **(D)** *Boiga cyanea,* **(E)** *B. guangxiensis,* **(F)** *B. multomaculata,* **(G)** *Calamaria pavimentata,* **(H)** *Coelognathus radiatus,* **(I)** *Dendrelaphis pictus,* **(J)** *Elaphe moellendorffi,* **(K)** *Elaphe taeniura,* **(L)** *Euprepiophis mandarinus,* **(M)** *Gonyosoma coeruleum,* **(N)** *G. frenatum,* **(O)** *Lycodon futsingensis,* **(P)** *L. meridionalis,* **(Q)** *Oligodon fasciolatus,* and **(R)** *Oreocryptophis porphyraceus.*

Fig. 7. Snake and turtle species recorded in Xuan Nha Nature Reserve, Vietnam: **(A)** *Ptyas korros*, **(B)** *Bungarus fasciatus*, **(C)** *Bungarus wanghaotingi*, **(D)** *Naja atra*, **(E)** *Sinomicrurus macclellandi*, **(F)** *Psammodynastes pulverulentus*, **(G)** *Hebius chapaensis*, **(H)** *Rhabdophis nigrocinctus*, **(I)** *Rhabdophis helleri*, **(J)** *Trimerodytes percarinatus*, **(K)** *Pareas hamptoni*, **(L)** *Ovophis monticola*, **(M)** *Trimeresurus albolabris*, **(N)** *Platysternon megacephalum*, and **(O)** *Manouria impressa*.

rows 19–19–15; ventrals 198; cloacal scale paired; subcaudals 100, paired. Coloration in preservative: dorsal surface green; belly greenish (determination after Liu et al. 2021).

Gonyosoma frenatum (Gray, 1853) (Fig. 6N): A road-killed specimen was found in the afternoon on Highway 6. The surrounding habitat was evergreen forest.

Lycodon futsingensis (Pope, 1928) (Fig. 6O): One specimen was found at night on the ground while moving near a stream in evergreen forest.

Lycodon meridionalis (Bourret, 1935) (Fig. 6P): A

road-killed specimen was found in the afternoon on Highway 6. The surrounding habitat was evergreen forest.

Oligodon fasciolatus (Günther, 1864) (Fig. 6Q): An individual was observed at night on the ground while moving across a forest trail, and a road-killed specimen was found on Highway 6. This is a new record for Xuan Nha NR.

Oreocryptophis porphyraceus (Cantor, 1839) (Fig. 6R): An individual was observed at night while moving on the roadside. The surrounding habitat was evergreen forest.

Ptyas korros (Schlegel, 1837) (Fig. 7A): Five individuals were found during the daytime on the ground or on tree branches near bamboo bushes, abandoned fields, and at the roadside near forest edge.

Elapidae

Bungarus fasciatus (Schneider, 1801) (Fig. 7B): An individual was observed at night near the ground by a stream at the forest edge.

Bungarus wanghaotingi Pope, 1928 (Fig. 7C): An individual was observed near a stream and another individual was observed in a rice field. The surrounding habitat was secondary forest. Previous records of *B. multicinctus* in Xuan Nha NR by Nguyen et al. (2010) and in Vietnam by Nguyen et al. (2009) should be re-identified as *Bungarus wanghaotingi* after Chen et al. (2021).

Naja atra Cantor, 1842 (Fig. 7D): An individual was observed in the afternoon on the ground, in a bamboo bush near Road 102. The surrounding habitat was the secondary forest.

Sinomicrurus macclellandi (Reinhardt, 1844) (Fig. 7E): A road-killed specimen was found in the morning on Highway 6. The surrounding habitat was evergreen forest.

Lamprophiidae

Psammodynastes pulverulentus (Boie, 1827) (Fig. 7F): An individual was observed at night on a tree branch near the forest edge.

Natricidae

Hebius chapaensis (Bourret, 1934) (Fig. G): One specimen was found at night in a stream in evergreen forest. This is a new record for Xuan Nha NR.

Rhabdophis nigrocinctus (Blyth, 1856) (Fig. 7H): One specimen was found in the afternoon while moving on the grass near a stream in secondary forest. This is a new record for Xuan Nha NR.

Rhabdophis helleri (Schmidt, 1925) (Fig. 7I): Individuals were found during the daytime on the ground or on grass near the roadside, and in rice fields. The surrounding habitat was secondary forest and agricultural cultivation areas.

Trimerodytes percarinatus (Boulenger, 1899) (Fig. 7J): An individual was observed in the afternoon near a stream. The surrounding habitat was evergreen forest.

Pareatidae

Pareas hamptoni (Boulenger, 1905) (Fig. 7K): One specimen was found at night sitting on a tree branch in evergreen forest. This is a new record for Xuan Nha NR.

Viperidae

Ovophis monticola (Günther, 1864) (Fig. 7L): One specimen was found at night while moving across a forest trail in evergreen forest.

Trimeresurus albolabris Gray, 1842 (Fig. 7M): Specimens were observed during the daytime on tree branches at forest edges. The surrounding habitat was secondary forest and agricultural cultivation areas.

Testudines
Platysternidae

Platysternon megacephalum Gray, 1831 (Fig. 7N): An individual was observed at night under a rock in a stream. The surrounding habitat was evergreen forest.

Testudinidae

Manouria impressa (Guenther, 1882) (Fig. 7O): An individual was observed in the afternoon under a wet carpet of leaves in evergreen forest.

Discussion

The new findings in this study bring the number of amphibian and reptile species in Xuan Nha NR to 107, comprising 41 amphibian and 66 reptile species, of which 21 species are new records for Xuan Nha NR, one species is a new record for Son La Province, and one is recorded for the first time from Vietnam. *Gonyosoma coeruleum* was recorded for the first time from outside of China based on a single specimen collected from Son La Province, Vietnam. This species was recently described by Liu et al. (2021) from Yunnan Province, China. Because of morphological ambiguity between *G. coeruleum* and *G. prasinum*, previous records of *G. prasinum* in Vietnam should be re-examined to determine whether they are referrable to *G. coeruleum* or are, in fact, true *G. prasinum*. *Hemiphyllodactylus bonkowskii* was recently described by Nguyen et al. (2020). Its original description was based on specimens found in Hoa Binh Province, with the type locality approximately 20 km from the new records in Xuan Nha NR.

Fig. 8. Threats to the herpetofauna in Xuan Nha Nature Reserve, Son La Province, Vietnam: **(A)** Slash and burn forest, **(B)** Illegal timber logging, **(C)** Domestic animal production in the forest, **(D, E)** Road-killed reptiles and amphibians on the road, and **(F)** Wildlife collection for food and trade.

Several of the records provided by Nguyen et al. (2010) were excluded from the list of Xuan Nha NR in this study, either because they were based on misidentifications or due to changes in taxonomy and/or nomenclature. For example, *Leptobrachella pelodytoides* was formerly reported from the nature reserve, but has since been assigned to a different taxon, and *L. pelodytoides* is considered to be restricted to Myanmar, southern China, and Thailand (Frost 2021). Previous records of *Leptobrachium chapaense, Amolops ricketti, Calotes mystaceus,* and *Bungarus multicinctus* in Xuan Nha NR, as reported by Nguyen et al. (2010), could be reidentified as *Leptobrachium masatakasatoi, Amolops cremnobatus, Calotes emma*, and *Bungarus wanghaotingi,* respectively. Some species were documented from Xuan Nha NR based on interview information only, viz. *Hylarana macrodactyla, Odorrana*

chloronota, Physignathus cocincinus, Varanus salvator, Python molurus, Ptyas mucosa, Ophiophagus hannah, Hypsiscopus plumbea, Fowlea flavipunctatus, Cuora mouhotii, Geoemyda spengleri, Mauremys sinensis, Indotestudo elongata, and *Palea steindachneri*. Nine other species (*Occidozyga lima, O. martensii, Hylarana taipehensis, Eutropis chapaensis, Amphiesma stolatum, Rhabdophis chrysargos, Trimeresurus stejnegeri, Cuora galbinifrons,* and *Sacalia quadriocellata*) were included in the list here based on the previous records of Nguyen et al. (2010).

In terms of habitat preferences, most of the amphibians and reptiles in this survey inhabit the evergreen forest (41 species, or 50% of the total recorded species), followed by disturbed secondary forest with 33 recorded species (40.24%), and agricultural areas with 19 recorded species (23.17%; Table 2).

Among the eight survey sites, Kho Hong has the highest level of species richness with 29 recorded species; followed by Lay forest with 26 species; the Hen Pin and Sao Do sites with 23 species; the Nga, Muong An and So Linh sites with 21 species; and Cong Troi with 15 species (Table 2). Both of the Kho Hong and Lay sites are located in the core zone of the Xuan Nha NR with a large area of evergreen forest (>3,000 hectares) and the habitat quality is relatively good. Therefore, the numbers of recorded species are higher than those of the other sites.

Concerning its herpetofaunal conservation status, the Xuan Nha NR harbors a high number of threatened species. Among the 107 species, 19 are listed in the Red Data Book of Vietnam (Dang et al. 2007), including three species categorized as CR, 10 as EN, and six as VU; 18 species are listed in the IUCN Red List (IUCN 2022), including six species categorized as CR, five as EN, five as VU, and two as NT; 14 species are listed in the Vietnam Governmental Decree No. 84/2021/ND-CP (2021), including three species in Group IB and 11 species in Group IIB; and 14 species are listed in the CITES appendices, including one species in Appendix I and 13 in Appendix II (Table 2). The major threats to the habitat and populations of amphibians and reptiles in the Xuan Nha NR are deforestation resulting from agricultural activities (Fig. 8A), illegal timber logging (Fig. 8B), free grazing of cattle in the forest (Fig. 8C), road construction (Fig. 8D–E), and wildlife poaching for food and trade (Fig. 8F).

Acknowledgements.—We are grateful to the directorates of Forest Protection Department of Son La Province and Xuan Nha Nature Reserve for their support of our field work and issuing relevant permits (permit No. 22/GT issued on 7 June 2012). We thank TA Sung, LA Sung, CA Sung, LA Sung (Van Ho District), and CV Nguyen and CA Lau (Moc Chau Chau District) for their assistance in the field.

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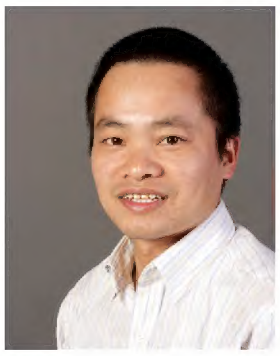

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